Ecological strategies of two Ranunculus species in relation to seasonal submergence

Thesis

Ecological strategies of two Ranunculus species in relation to seasonal submergence.

A thesis submitted to the Open University in partial fulfillment for a PhD in plant ecology by Stephen John Smith, BSc, PGCE.

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Abstract

This thesis is concerned with the role of submergence in the ecology of the perennial Ranunculus repens and the annual R. sceleratus, both of which are common in seasonally submerged habitats. Evidence is presented for genetic differentiation between R. repens populations with respect to tactical changes in allocation and growth form in response to submergence. R. repens plants maintain or increase their dry weight allocation to stolons in response to submergence independent of site of origin. A decrease in flowering in submerged R. repens plants was related to a change in the positive correlation between total dry weight and the probability of flowering in these plants. The dry weight per unit length of petioles decreased in response to submergence in plants from all sites but changes in the dry weight per unit length of stolons depended on the site of origin of the plants. Plants from all sites showed plasticity in growth form with respect to stolon internode lengths but the direction of change in response to submergence depended on site.

At low nutrient levels R. sceleratus plants showed increased dry weight allocation to vegetative organs in response to submergence but unchanged or reduced allocation to sexual reproductive structures. However, all changes in allocation in response to submergence disappeared at higher nutrient levels. Reductions in the number of flowers per plant in response to submergence were independent of nutrient status but plants at high nutrient levels showed no change in the number of seeds per plant due to a larger number of seeds per seed head. This may be related to the association of this species with nutrient rich habitats. A demographic analysis of R. sceleratus showed that these plants can exhibit a wide range of life history tactics. There was a trend for a longer pre-flowering period to result in lower survivorship but greater seed output. Seed germination in this species is promoted by diurnally fluctuating temperatures in both the light and dark but the promotion is greatest in the former. -

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Contents

List of tables

List of figures

"..the only real strategists .. are evolutionary theorists.."

(Ghiselin, 1974:41)

Chapter 1

Ecological Strategies

> "The words 'strategy' and 'tactic' have become commonplace in ecological ... discourse, but their meanings and connotations as theoretical constructs are not clear."
>
> (Istock, 1984:161)

1.1 What is meant by the term strategy in ecology?

The word strategy is found, often without definition, throughout ecological literature. An idea of the breadth of its usage can be seen from the following selected references: thermoregulation strategies (Stevenson, 1985), regeneration strategies (Grime, 1979), allocation strategies (Hickman, 1975), demographic strategies (Klemow and Raynal, 1983), nest-site choice strategies (Monaghan, 1982), colonisation strategies (MacArthur and Wilson, 1967), seed germination strategies (Mayer and Poljakoff-Mayber, 1975), life history strategies (Wilbur, 1976) and reproductive strategies (Bostock and Benton, 1979). In many of the above references the word strategy was used without definition - so what exactly is meant by the term strategy?

The Longman Dictionary of the English Language (1984) defines strategy as 'the art of devising or employing plans towards achieving a goal'. If this use of the word strategy is taken in ecological literature where it is undefined, this is clear evidence of teleology (Harper, 1982).

However, Ghiselin (1974) points out that the word strategy is used in a past sense, that is, organisms have strategies that have been successful. Harper (1982) puts it neatly 'a strategy is a property that is by, with or from the past'. Harper (1982) goes on to say that in most ecological writing the 'goal-centred' use of strategy is implied.

Some authors (Grime, 1979; Harper, 1982; Silvertown, 1982, Waite and Hutchings, 1982) do give definitions of their use of the term strategy. Grime (1979) defines it as 'groupings of similar or analogous genetic characteristics which recur widely among species or populations and cause them to exhibit similarities in ecology', whereas Harper (1982) refers to a strategy as 'the programmed biology, especially the life cycle, of an organism' and Silvertown (1982) as 'a set of correlated life history characters'.

Waite and Hutchings (1982) define strategy as 'a collection of co-evolved traits, each of which has been subjected to selective forces which tend to maximise the fitness of the individual'. Confusingly the term 'tactics' (which will be discussed later) is used by Stearns (1976) to mean something very similar '...a set of coadapted traits designed, by natural selection to solve particular ecological problems .. a complex adaptation', it is also clear from Stearns (1976; 1977) that his term tactics is synonymous with the term strategy (Istock, 1984).

The latter two definitions imply increased fitness conferred on the organism by possession of a particular strategy but the term strategy is often used when no evidence of increased fitness is given or even assumed. No increase in fitness is stated or implied in the other four definitions. Four of the the above definitions suggest that the components of a strategy are either correlated, co-adapted, similar or

analogous but again this criterion is rarely tested or even assumed.

The author proposes a definition of strategy as 'any set of traits, attributes or characteristics of an organism in a defined area of study', e.g. allocation, growth form, demography, etc. This does not leave the term useless as it can still be used as shorthand for a set of characteristics and help their classification. ' What this definition does is to remove the assumed or implied increase in fitness conferred on an organism by the possession of a particular strategy and the assumed or implied correlation of the various traits. This latter definition will be implied when the term strategy is used unless stated otherwise.

1.2 Strategy versus tactics

Strategies are a function of the genotype of an organism (Harper and Ogden, 1970; Hickman, 1975; Harper, 1977; Thompson and Stewart, 1981; Waite and Hutchings, 1982). Plastic responses due to the environment are often called 'tactics' (Harper, 1977; Waite and Hutchings, 1982). Unless a distinction between environment and genotype effects has been clearly made, results are inadmissable for discussions of strategies. Genotype-environment effects are often separated by working within in a common environment (see for example, Douglas, 1981; Reinartz, 1984b)

Thompson and Stewart (1981) sum up research on reproductive strategies where no attempts to separate genotype and environment effects have been made as follows '..the results of those investigators who measured reproductive effort solely in the field ... add little to our understanding of reproductive strategies'. The need to separate these

effects is emphasised by several studies where field differences have disappeared under common environments (Hickman, 1975; Abrahamson and Hershey, 1977; Raynal, 1979).

The strategy, set by the genotype, also defines the range of tactics shown (Harper and Ogden, 1970; Harper, 1977). Tactical changes can be used to describe a strategy as long as strategy and tactics (genotype and environment) have been clearly separated (Grime, 1979; Thompson and Stewart, 1981; Waite and Hutchings, 1982).

This research project is concerned with the strategies and tactics shown by plants growing in seasonally submerged environments. The research was centred on allocation, demographic and growth form strategies, and tactical variations within them.

1.3 Allocation theory

Many authors (e.g. Harper and Ogden, 1970; Thompson and Stewart, 1981; Waite and Hutchings, 1982) attribute the concept of allocation to Cody (1966). He considered organisms as having a limited amount of time or energy and that natural selection will operate on the allocation of these resources to maximise the contribution of the genotype to the following generations.

He called this the "principle of allocation" and attributed it to an unpublished paper of Levins and MacArthur. This concept is implicit in the writings of MacArthur and Wilson (1967) (see Sarukhan, 1976; Thompson and Stewart, 1981). Cody's concept of allocation is the foundation of the study of allocation strategies (Harper, 1977).

Two different streams of research follow this original concept. Firstly, MacArthur and Wilson (1967) developed the so-called 'r-K selection' model of life history strategies. The crux of this is that organisms growing under conditions where density independent mortality operates will show a suite of traits which includes high allocation to (sexual) reproduction; they termed this r-selection. Whereas under conditions of density dependent mortality organisms will show a different suite of traits including low allocation to reproduction; this was termed K-selection. This was later modified by Pianka (1970) who introduced the idea of an r-K selection continuum.

Later Gadgil and Solbrig (1972) introduced the terms r and K strategists for the two extremes. They go on to state that '...the crucial evidence needed for r- and K- selection is whether an organism is allocating a greater proportion of its resources to reproductive activities (r-strategists) than another related one (K-strategist) under any and all D.D. (density dependent) and D.I. (density independent) mortality conditions'.

This assessment criterion has been used by many researchers and numerous studies comparing the allocation of resources to reproduction within plant species have followed, e.g. Taraxacum (Gadgil and Solbrig, 1972; Solbrig and Simpson, 1974; 1977), Typha (McNaughton, 1975), Helianthus (Gaines et al, 1974), Solidago (Abrahamson and Gadgil, 1973), Polygonum (Hickman, 1975; 1977), Rubus (Abrahamson, 1975a; 1975b), Allium (Kawano and Nagai, 1975).

However, in several of these studies (Abrahamson and Gadgil, 1973; Abrahamson, 1975a; 1975b; 1979; Gaines et al, 1974) plants were not grown in a common environment and so their results are of limited value

in a discussion of reproductive strategies (Thompson and Stewart, 1981; and see section 1.2). This was ably demonstrated by Hickman (1975) when field measurements of reproductive allocation in Polygonum cascadense gave results that fitted the r-K selection model but these differences disappeared when the plants were grown in common environments. Abrahamson and Hershey (1977), and Raynal (1979) also found that field differences in allocation disappeared under a common environment. Stearns (1977), in reviewing all the data on r-K selection for both animals and plants, came to the conclusion that more work was required before the theory could be accepted or rejected.

A second stream, independent of the work on r-K selection, but also having its origins in the "principle of allocation" (Cody, 1966) is the study of strategic and tactical allocation in plants (with special reference to reproductive allocation) introduced in Harper (1967). The initial research was carried out by Harper and Ogden (1970: but see also Ogden, 1968).

This work was carried on by many researchers, e.g. Ginzo and Lovell (1973a), Ogden (1974), Sarukhan (1976), Andel and Vera (1977), Lovett Doust (1980), Waite and Hutchings (1982) and Kawano and Miyake (1983). Evidence for the divergence of these two streams can be seen in the differences in terminology (see Chapter 2) evident in the key papers of Gadgil and Solbrig (1972), and Harper and Ogden (1970) noted by Thompson and Stewart (1981).

1.4 Criticisms of Cody's allocation model

Cody's model has two basic assumptions: that energy is limiting and that

vegetative and reproduction allocation are competing functions (Harper, 1967; 1977; Abrahamson and Caswell, 1982). The first assumption, that energy (which is usually expressed in terms of dry weight; see section 2.1) is limiting, has been criticised because nutrients which may limit growth can show different allocation patterns to those for energy (Chapin, 1980; Lovett Doust, 1980; Abrahamson and Caswell, 1982).

Abrahamson and Caswell (1982) carried out a study on the allocation of various resources in Verbascum thapsus and Solidago spp. and concluded that '..on the basis of the results ... we cannot identify a crucial resource..' and '..it can .. be argued that biomass (= energy; see section 2.1) is a reasonable currency to measure allocation patterns... however, the crucial question remains of what parameters actually limit allocation..'

Earlier, Harper (1977) stated that '...the detailed patterns of allocation of resources are very difficult to follow in a plant ... and it is difficult to decide which resource is appropriate to follow. Partly because it is the easiest and partly following the example of Cody, the few comparisons of allocation have been made for energy or dry weight...'. Thompson and Stewart (1981) suggest that further research is required before conclusions about limiting factors can be reached.

The second assumption, that vegetative and reproduction allocation are competing functions has also been criticised (Bazzaz and Carlson, 1979). However, the presence of developing fruits has been shown to reduce or stop vegetative growth and increase leaf senescence (Chapin, 1980).

Harper (1977) again summarises the available evidence '...physiological information generally supports the idea that there are limited resources

available to a growing plant that are allocated between seed products and other activities...'. Again more research is required before this assumption can be rejected (Thompson and Stewart, 1981).

Much of the initial work on allocation strategies in plants was carried out on dry weight (as estimates of energy) (Ogden, 1968; Harper and Ogden, 1970; Gadgil and Solbrig, 1972) and later workers have carried on this methodology (e.g. Bostock and Benton, 1979; Waite and Hutchings, 1982; Reinartz, 1984b; see Chapter 2).

It is clear from recent literature (e.g. Brock, 1983; Kawano and Miyake, 1983; Reinartz, 1984b; Pitelka et al, 1985) that dry weight allocation patterns in plants are still considered to be of strategic and tactical importance.

1.5 Demographic strategies

Demography is principally concerned with the timing of births and deaths. Deevey (1947) proposed three basic patterns of mortality with time: Type I where there is little juvenile mortality and adult mortality is confined to a short time period, Type II where mortality is spread throughout juvenile and adult stages and Type III where mortality is concentrated in the juvenile stage.

Deevey's classification was a summary of earlier work on animal survivorship (Pearl and Miner, 1935). However, work on plant survivorship did not take off until the early 1970's (Williams, 1970; Sharitz and McCormick, 1973; Sarukhan and Harper, 1973) but dominates ecology in the early 1980's (at least in Britain).

The timing of flowering, and therefore of seed production, has also been of considerable interest (Harper, 1977). Recently there has been interest in the classification of plants by the timing of flowering and death, in particular the concept of the "biennial" has been reviewed (Reinartz, 1984a; Silvertown, 1984; Kelly, 1985).

The pattern of survivorship can be related to flowering behaviour. Perennial plants often show patterns which lie between Deevey Types II and III (Harper, 1977; Silvertown, 1982). Annuals often show Deevey Type I survivorship patterns (Silvertown, 1982). However, Watkinson and Harper (1978), and Klemow and Raynal (1983) have suggested that annuals can be divided into two groups based on their survivorship pattern, fecundity and survival of seed in the seed bank. Clearly, life history and demographic strategies are closely linked.

1.6 Growth Form Strategies

Over recent years there has been growing interest in plant growth form and 'adaptive architecture' (Bell and Tomlinson, 1980). Much of this work has centred on trees (Halle et al, 1978; Maillette, 1982a; 1982b) and clonal perennials (Bell, 1974; 1979; 1980; Lovett Doust, 1981a; Hartnett and Bazzaz, 1985a; 1985b; 1985c; Dickerman and Wetzel, 1985). The results suggest that plant growth form can be described in a series of "rules", such as branching angle, inter-metamer (the basic structural unit: see Harper, 1977) distances, and the probabilities of metamer survival, growth, flowering, etc. (Bell et al, 1979).

Lovett Doust (1981a) and Harper (1981) have introduced the terms phalanx and guerilla to describe the growth form of clonal perennials (but see

Clegg, 1978). The phalanx growth form is where the ramets (or 'daughters'; the units of iteration of a clonal perennial) are densely packed and make little contact with other plants. The guerilla growth form describes loosely packed ramets making a large number of contacts with other plants. The terms are used relatively and clonal perennials can be placed on a phalanx-guerilla continuum (Bulow-Olsen et al, 1984).

1.7 Seasonal Submergence

As mentioned earlier this work is centred on the strategies and tactics shown by plants subject to seasonal submergence. Seasonal submergence results in plants having to survive and grow in both terrestrial and aquatic environments.

Flooding of the soil results in both reduced soil oxygen levels and nutrient availability (Sanderson and Armstrong, 1980; Kozlowski, 1984a). Submergence includes soil flooding, but also involves the immersion of normally aerial parts which results in features such as decreased availability of gaseous carbon dioxide (Maberly and Spence, 1983).

Much research has been carried out on soil flooding and plant growth. Some of this work has been carried out from the point of view of the biochemistry of roots in flooded soils and mechanisms of flooding tolerance (e.g. Crawford, 1978; 1982; Smith and Rees, 1979; Keeley, 1979; Jackson et al, 1982). Other studies have concentrated on morphological aspects of plant growth in flooded soils (e.g. Wample and Reid, 1978; Drew et al, 1979; 1980).

Work on the biochemistry of flooded roots has led Crawford and his co-

workers (see Crawford, 1978; 1982) to propose that the roots of flood tolerant plants have a modified root biochemistry. Crawford proposes that the avoidance of the build up of the toxic products of anaerobic respiration, such as ethanol, results in flood tolerance.

This system is challenged by Jackson et al (1982) because the levels of ethanol found in plants which die as a result of flooding are not, in themselves, high enough to result in plant death. Other workers have challenged Crawford's hypothesis; Smith and Rees (1979) were unable to find end-products of anaerobic respiration, other than ethanol in either tolerant or intolerant species and Keeley (1979) found that other end-products (e.g. malate) accumulated independently of ethanol.

The work of Keeley (1979) on Nyssa sylvatica has shown that genetic differentiation can occur within a species in response to a flooding gradient. He found that plants from dry, upland sites showed little or no physiological modification to flooded soils, whereas plants from a site flooded most of the year showed marked changes in root physiology and plants from a seasonally flooded flood-plain showed changes in root physiology that were intermediate between these two extremes.

The plants that show the above features would be classified by Levitt (1975) as stress tolerators because they tolerate the low oxygen conditions resulting from the soil flooding. Stress avoiders (Levitt, 1975), however, prevent the hypoxic conditions from occurring. These plants include those that possess a root aeration system; this often involves an increase in the air-spaces in shoots and roots, the aerenchyma tissue (Arber, 1920). There has been, and still is, considerable debate over the function of aerenchyma tissue (see for example Vallance and Coult, 1958; Williams and Barber, 1961; Hook et al,

1971; Armstrong, 1978; Dacey, 1981; Crawford, 1982) but it is probable that at least one of its functions is the delivery of oxygen to underground structures (e.g. Dacey, 1981).

Other aeration systems include the development of adventitious roots just above the surface of the flooded soil (or water); these have been found in trees (Gill, 1970; 1975; Clemens et al, 1978; Kozlowski, 1984b), Zea mays (Drew et al, 1979; Wenkert et al, 1981) and Epilobium hirsutum (Etherington, 1983). Rice plants solve the problem of nutrient deficiency and toxicity resulting from hypoxic soil conditions (Gambrell and Patrick, 1978) by oxygenating their rhizospheres (Green and Etherington, 1977). This has also been found in the roots of Nyssa aquatica (Hook and Scholtens, 1978) and proposed for Schoenoplectus lacustris rhizomes (Haldemann and Brandle, 1983).

Submergence of the normally aerial parts means that the whole plant will have reduced gaseous supply. This will be a particular problem for plants with an aerial oxygenation system, since (if submergence is complete) this will cease to operate. This can be seen from experiments reported in Haslam (1972) where Phragmites communis yield reductions due to harvest the previous year were much greater when the stubble was submerged following harvest.

Aquatic plants show many features which can be related to their submerged habit, such as increased aerenchyma tissue (see above), and modified photosynthesis (Keeley, 1983). Another feature shown by some aquatic plants is the so-called 'depth accommodation response' (Arber, 1920; Sculthorpe, 1967), whereby aerial organs, such as petioles, rachis, stems and flowering stems, elongate in response to submergence (Ridge and Amarasinghe, 1984).

The physiological basis of this response has been studied in several species and involves ethylene (Cookson and Osborne, 1978) which builds up in the submerged tissues due to reduced diffusion of the gas in water (Musgrave et al, 1972). Ethylene, under the right hormonal background, stimulates either cell expansion and cell division or just cell expansion (Funke and Bartels, 1937; Musgrave et al, 1972; Musgrave and Walters, 1974; Malone and Ridge, 1983; Cookson and Osborne, 1978; Ridge, 1985; Ridge and Amarasinghe, 1984).

This response to ethylene in aquatic species is different from that of many terrestrial species where ethylene is often a growth inhibitor (see for example Wareing and Phillips, 1981). However, the depth accommodation response has been found in floating leaved aquatics (e.g Nymphaea alba; Gessner, 1959, Nymphoides peltata; Malone and Ridge, 1983), mud colonisers (e.g. Ranunculus sceleratus; Cookson and Osborne, 1978) and damp pasture plants (e.g. Ranunculus repens; Ridge, 1985).

Although all these species have been shown to respond to submergence by elongation, the **amount** and **rate** of response varies enormously. Ridge (unpublished) has classified the elongation responses of plants to submergence into three groups (four if neutral plants are included).

Group one plants show a large response and no delay; group two plants show a large to medium response but with some delay and group three plants show a small response with a marked delay. The rate and amount of response can be related to habitat (the probability of submergence and its duration) and life history.

1.8 Stress response strategies

In general the term 'stress' is used to mean any external factor that is considered to be sub-optimal for plant growth (e.g. Etherington, 1983). Physiologists have studied the response of plants to sub-optimal environmental factors for many years and much of this work is reviewed in Levitt (1975). Levitt (1975) considers stress to be any environmental factor capable of inducing a potentially injurious chemical or physical change in living organisms. Levitt (1975) defines injury as a specified level of damage; often death of 50% of the plant.

This definition excludes external factors (such as light, carbon dioxide and nutrients) which when sub-optimal do not necessarily result in injury but are ecologically meaningful. Therefore, it is not suprising that Grime (1979) when discussing stress from an ecological standpoint defines it to include such factors. He defines stress as 'external constraints which limit the rate of dry matter production of all or part of the vegetation'.

Grime (1979) divides plants into three main types based on their response to stress; ruderals, competitors and stress-tolerators. Ruderals respond to stress by rapid curtailment of vegetative growth and the diversion of resources into seed production. Ruderals tend to have relatively short life-cycles and many of them are annuals.

Competitors respond to stress by large and rapid changes in morphology. Life-cycles of competitors vary from relatively short to relatively long; usually more than one year. Stress-tolerators respond to stress with small and slow changes in morphology; seed production is often terminated. The life-cycle of stress-tolerators tends to be relatively

long.

Grime (1979) has attempted to relate this system to the r-K selection model of life-history strategies of MacArthur and Wilson (1967) (see section 1.3). He suggests that ruderals and stress-tolerators represent, respectively, the r- and K-selected poles of the r-K continuum, with competitors falling in an intermediate position.

The work of Hickman (1975) with Polygonum cascadense highlights problems with this interpretation. Hickman (1975) found that Polygonum plants in the field increased their allocation to seed (see section 2.1) with increased stress (mainly drought and density) and appeared to be an example of an r-strategist. These differences disappeared under a common environment and so Hickman (rightly) concluded that this was not an example of an r-strategist. It is, however, an example of a ruderal-type response to stress.

Grime's (1979) model is based on tactical changes in allocation whereas the r-K strategic model is based on genetically-fixed differences in allocation (Gadgil and Solbrig, 1972). Grime (1979:46) sums this up '...a critical genetic [i.e. strategic] difference between competitive, stress-tolerant, and ruderal plants concerns the form and extent of phenotypic [i.e.tactical] response to stress...' (bracketed words added).

Differences or changes in allocation, demographic or growth form strategies and tactics in relation to seasonal submergence can be interpreted as part of an overall stress response strategy.

1.9 Aims of this project

The overal aim of this project was to study the ecology in relation to submergence of an annual (Ranunculus sceleratus) and a perennial (R. repens) both of which are found in areas subjected to seasonal submegence. The more specific aims were:

- to study tactical changes in dry weight allocation in relation to submergence in both the annual and the perennial.
- to study genetic differentiation between populations of the perennial with respect to seasonal submergence.
- to study the plasticity in the growth form of the perennial in relation to submergence.
- to study the changes in flowering behaviour of the perennial in relation to submergence.
- to study the changes in dry weight distributions in stolons and petioles in the perennial in relation to submergence.
- to study the interaction of nutrient level and submergence in the annual.
- to study the demography of the annual in a habitat subjected to seasonal submergence.
- to study the seed germination of the annual, especially in relation to submergence.

1.10 Summary

1. The term "strategy" is ill-defined in ecological literature.

2. Genetic and phenotypic components of a response must be distinguished

in discussions of strategy.

3. Allocation theory is generally attributed to Cody (1966) and two main lines of research follow from this paper.

4. Allocation theory can be criticised on fundamental grounds.

5. Although there has been much research on the effects of soil flooding on plant growth little work has been carried out on submergence.

6. It is possible that submergence can be regarded as a "stress" and the response of plants compared to other stress response strategies.

Chapter 2

Methodology

"Arbitrary decisions have to be made if plant populations are to become numerable and the arbitrariness of the decisions has often discouraged attempts to count plants"

(Harper, 1967).

2.1 Introduction

From Chapter 1 it can be seen that the "principle of allocation" of Cody (1966) can be criticised on fundamental grounds but it also has complex methodological problems. The first is: how can energy allocation be easily measured? Gadgil and Solbrig (1972) assumed that dry weight allocation was similar to net energy allocation and so measured allocation in terms of dry weights. Harper and Ogden (1970) measured both net energy allocation (using a calorimeter) and dry weight allocation and concluded that the former was unnecessary and so most researchers have carried on the same way. Hickman and Pitelka (1975) showed that the allocation patterns for net energy and dry weight were similar for Polygonum cascadense, and this is often used to justify the use of dry weight allocation patterns as indicative of net energy allocation patterns (e.g Reinartz, 1984b). More recent work (Abrahamson and Caswell, 1982) has supported the findings of Hickman and Pitelka (1975).

Secondly, what is meant by allocation to reproduction as opposed to vegetative allocation? Harper and Ogden (1970) take the dry weight of "seeds" (as is common in ecological literature, e.g. Silvertown (1981), Grime et al (1981), Salisbury (1942), the term seed refers to the dispersal unit of the plant which may technically be a fruit) to be reproductive allocation. However, Gadgil and Solbrig (1972) take reproductive allocation to be the dry weight of "all reproductive structures". Research following these papers has fallen into two sets - those who use reproductive allocation to mean seed allocation (e.g Ogden, 1974, Sarukhan, 1976) and those who use reproductive allocation to mean "all reproductive structures" (e.g. Waite and Hutchings, 1982).

Thompson and Stewart (1981) contend that Gadgil and Solbrig (1972) were more in line with Cody's original concept by taking reproductive allocation to be "all reproductive structures". But there is a further problem; what constitutes a "reproductive structure"? Most authors who have used the term "all reproductive structures" have considered floral structures and have excluded flowering stems and other supporting organs (Thompson and Stewart, 1981). However, some authors have included supporting structures, such as flowering stems, e.g. Hawthorn and Cavers (1978) and Waite and Hutchings (1982).

The overall problem is that "reproductive allocation" data are very difficult to compare because of wide differences in methodology. Clearly, the dividing line between vegetative and reproductive allocation is rather arbitrary and therefore researcher-dependent.

One very interesting development was introduced by Bostock and Benton (1979) who defined levels of reproductive allocation. These were allocation to embryos ("primary reproductive allocation"), allocation to

fruits sensu stricto ("secondary reproductive allocation") and allocation to other "floral structures" such as peduncles, perianth etc. ("tertiary reproductive allocation").

Another methodological problem is concerned with the variation in reproductive allocation with phenology. Generally reproductive allocation (within a season) increases with time to a maximum and then falls (Harper and Ogden, 1970; Gadgil and Solbrig, 1972) and as most authors are concerned with this maximum, serial harvests have been conducted to find these maxima (Harper and Ogden, 1970; Douglas, 1981). However, serial harvests are very time consuming and costly in terms of replication and so many authors harvest at an arbitrarily defined "maturity" (e.g. Gaines et al, 1974; Reinartz, 1984b).

The results of allocation studies are usually presented as the dry weight (or calorific content) of a particular organ as a percentage of the total dry weight (or calorific content) of the plant. However, some studies have ignored underground material (e.g. Gaines et al, 1974; Waite and Hutchings, 1982) and express results as a percentage of total aboveground dry weight (or calorific content). This difference must be borne in mind when comparing results.

It is obvious from this section that allocation studies require several rather arbitrary decisions but so do demographic studies (Harper 1967). These decisions include, for example, the choice of sampling interval. In general the shorter the sampling interval the more accurate the numeration of plants. The appropriate interval will vary with species and site, depending on the stability of the population and site. The sampling interval for a range of annuals varied from 2 to 6 weeks (Keddy, 1982; Burdon et al, 1983; Klemow and Raynal, 1983; Mack

and Pyke, 1983).

Before the methods section (2.4), the species used in this study will be described along with reasons for their choice.

2.2 Species studied

The plant species studied were Ranunculus sceleratus L. (Celery-leaved Buttercup or Celery-leaved Crowfoot) and Ranunculus repens L. (Creeping Buttercup).

2.2.1 Ranunculus sceleratus

Ranunculus sceleratus is a short-lived (ephemeral, annual or "biennial") herbaceous plant commonly found on exposed, bare or disturbed mud on the margins of rivers, lakes and ponds (Toorn, 1980; Fitter, 1978; Clapham et al, 1981; Salisbury, 1970). Many of these areas are subject to seasonal submergence and it has been shown that the petioles and flowering stems show the depth accommodation response (Cookson and Osborne, 1978; Samarakoon and Horton, 1981).

Vegetative growth is in the form of a rosette of palmate leaves. A hollow, much-branched flowering stem is produced from the centre of this rosette. The small (c. 5mm), inconspicuous yellow flowers produce a mass of small achenes (c. 0.15mg). Flowering, which takes place from June-August (Clapham et al, 1981), has been shown to be under Long Day control in plants of Canadian origin (Samarakoon and Horton, 1981).

This plant is very plastic; literature values of flowering stem height vary from 5 cm to 120 cm (Salisbury, 1970; Toorn, 1980) and seed output per plant is also very variable, values of 15,000 - 500,000 have been reported in the literature (Salisbury, 1942; Toorn, 1980). Seed germination has been reported to be promoted by diurnal fluctuations in temperature (Mayer and Poljakoff-Mayber, 1975). Seedling emergence takes place in the spring and autumn (Whitehead, 1971; Toorn, 1980).

2.2.2 Ranunculus repens

Ranunculus repens is a herbaceous clonal perennial which reproduces vegetatively by the production of daughter rosettes (or ramets) borne on stolons (Harper, 1957; Darlington and Brown, 1975; Lovett Doust, 1981a; Clapham et al, 1981; Coles, 1977). It is common in damp pastures, marshes, woodland clearings and open waste-land but it is usually absent from dry grasslands (Harper, 1957).

Conspicuous yellow flowers are borne on flowering stems produced either from the vegetative rosettes or from the daughter rosettes. Achenes are relatively large (c. 2.30mg) and, like R. sceleratus, germination is promoted by diurnal fluctuations in temperature (Thompson and Grime, 1983). Seedling emergence mainly takes place in the spring (Harper, 1977). The petioles of this species have also been shown to exhibit the depth accommodation response (Ridge, 1984).

A large amount of demographic data has been collected for this species (possibly more than any other plant!) (Sarukhan, 1970; 1971; 1974; Sarukhan and Harper, 1973; Sarukhan and Gadgil, 1974; Clegg, 1978; Lovett-Doust, 1981a; 1981b; 1981c; Soane and Watkinson, 1979); this will

be discussed later.

The terminology used in discussions of clonal perennials, such as R. repens, is confusing and complex. The term "ramet" (Harper, 1977) is used to refer to the vegetatively produced, genetically identical (or at least very, similar - see Lovett Doust, 1981c; Hunt, 1984) "daughters" that are borne on stolons and/or rhizomes. If ramets are attached directly to the "parent" then they are referred to as "tillers" (e.g. in grasses).

Another term used in discussions of clonal perennials is "metamer" (Harper, 1977). This can be used to refer to ramets but also includes the stolon (or stolon bud) associated with the "daughter" plant. This difference is high lighted by the use of the term metamer (Harper, 1977) for the iterative units of, for example, trees (leaf plus axillary bud) where the term ramet is inappropriate as the iterative units do not normally become independent of the "parent". A term which is synonymous with metamer is "module".

A collection of modules, metamers or ramets from the same "parent", whether attached or not, is termed a "genet" (Harper, 1977). The term "clone" has a similar meaning to genet but usually refers to attached modules, metamers or ramets.

2.3 Why study these two species?

1. Both species are commonly found in areas subject to seasonal submergence (Harper, 1957; Toorn, 1980; Salisbury, 1970).

2. Petioles of both species are known to show the "depth accommodation response" (Cookson and Osborne, 1978; Ridge, 1985). R. sceleratus flowering stems also show this response (Samarakoon and Horton, 1981).

3. They have contrasting life history strategies (annual/perennial), thus providing an opportunity for comparison.

4. They have different reproductive strategies. R. repens reproduces by seed and ramets and R. sceleratus by seed alone.

5. There is a substantial body of literature for both species which is invaluable in planning future research.

6. Both species are easy to obtain locally and easily cultivated.

2.4 Synopses and methodologies for experiments.

2.4.1 Ranunculus repens experiments

Synopsis of Experiment 1

The initial R. repens experiment was started during November 1981 and involved the comparison of air-grown and submerged plants. This experiment was designed to study the changes in both allocation and phenology resulting from submergence. Locally collected R. repens plants were used, not plants from a known submerged site.

Methodology for Experiment 1

Forty-two rosettes of Ranunculus repens, each with four mature leaves and a rosette diameter of 3 to 4cm, were collected from a single grassland site in Walton Hall, Milton Keynes on 4th November 1981. Two rosettes were transplanted into each of twenty-one trays (30 x 20 x 5cm) containing Levingtons potting compost over a thin layer of washed pebbles. The plants were left to acclimatize in the greenhouse for two weeks. A 16hr photoperiod was maintained, daylight being supplemented by a bank of three Thorn PAR mercury vapour lamps. The temperature was maintained at 20°C. These conditions were kept throughout the experiment.

After two weeks six rosettes were harvested and treated as described below to act as time-zero controls. Twenty-four rosettes (twelve trays) were placed into four aquarium tanks (130 x 50 x 50cm), six rosettes per tank. The tanks were then filled with water so that there was 15cm depth of water above the soil surface in the trays; this was increased to 20cm after the first week because leaves of many of the plants reached almost to the water surface. Two of these tanks were kept full of water for 13 weeks, the whole length of the experiment. The other two tanks were drained after 5 weeks and the plants allowed to grow in air until the end of the experiment. Twelve rosettes (six trays) were regularly watered and left to drain freely throughout the experiment to act as controls.

After 13 weeks all plants were harvested, the plants being divided into underground structures, leaves, petioles, stolons, and ramets. The plant material was then dried at 60°C until constant weight (about 4 days). Before drying the lengths of petioles were measured.

Synopsis of Experiment 2

This experiment was similar to Experiment 1 but was set up outside during March 1982 to look at changes resulting from submergence under "field" conditions. The experiment lasted for 16 weeks and involved comparisons between 16 week air-grown controls, 12 week submerged/4 week air-grown and 4 week submerged/12 week air-grown plants. Again locally collected R. repens plants were used. Of particular interest was the demography of leaves and stolons, and the balance of asexual and sexual reproduction.

Methodology for Experiment 2

The number and arrangement of plants was as in Experiment 1, with 42 plants placed in pairs into 21 trays. As in Experiment 1, twenty-four plants were placed into tanks and submerged to a depth of 20cm. After 4 weeks twelve plants were drained and left to grow in air, and the remainder were left until after 12 weeks and then drained. Twelve plants were used as controls, and were regularly watered. Six plants were harvested as time-zero controls.

At the start of the experiment all the petioles were marked by placing a 5mm piece of plastic straw carefully around them. At weekly intervals new petioles were marked with different coloured pieces of plastic straw and the loss of earlier marked petioles was recorded. This system allowed for the monitoring of the petiole/leaf demography during the experiment under the different treatments; the monitoring was stopped after 12 weeks. Stolons were marked in a similar way.

After 16 weeks the plants were harvested and weighed as in Experiment 1

and the lengths of stolons and petioles were measured.

Synopsis of Experiment 3

This experiment was designed to look at the influence of plant origin on response to submergence. Rosettes were collected from three sites, one regularly submerged, another, a few metres away, occasionally submerged and a third rarely submerged site some miles from the first two sites (see Appendix 1). This third site was the source of the material used in experiments 1 and 2. The experiment took place during 1983. The rosettes were submerged during February for four weeks, air controls being kept in moist soil during this time. The experiment finished during early August.

Methodology for Experiment 3

During the second week of January 1983, twenty rosettes of R. repens were collected from each of three sites (further details in Appendix 1). The principles behind the criteria for selection of rosettes were that the rosettes collected within each site had to be as morphologically similar as possible (based on the number of leaves and rosette diameter) and the largest plants available. Plants from the different sites varied considerably in appearance and so different selection criteria were introduced in the different sites (Table 2.1).

The sixty plants were individually potted into 15cm diameter pots containing John Innes no. 2 compost. The pots were then left outside to acclimatize for two weeks. After this time ten plants from each site were placed into tanks and submerged to a depth of 20cm whilst the other 10 were left, as controls, in shallow trays which allowed the compost in

Table 2.1

Criteria for collection of *R. repens* rosettes from the three field sites in January 1983 for experiment 3.

Site	Number of leaves/plant	Rosette diameter (cm)
Port Meadow submerged	2	6.0 - 7.0 **
Port Meadow non-submerged	3	.2.0 - 4.0
Open University	4	2.0 - 4.0

** Rosette diameter based on sum of the lengths of both petioles.

the pots to be kept permanently moist. After 4 weeks the water level in the tanks was lowered and conditions as in the controls were imposed.

During the first week in May the plants were carefully transplanted into 27cm diameter plastic pots to allow for greater vegetative spread. During the second week of August the plants were harvested and weighed as in Experiment 1. Measurements of petiole lengths, stolon lengths and stolon internode lengths were also made. During the experiment the number of flowers/plant was also recorded.

The choice of harvest time in allocation studies is to some extent arbitrary (see section 2.1). In this case it was chosen with two aims in mind. Firstly, to allow the plants to complete flowering and secondly, to be as close as possible to Peak Standing Crop (PSC) (maximum dry weight) as a measure of "maturity" (section 2.1). Sarukhan (1976) found PSC in R. repens to be in early July and as flowering occurs from May to August (Clapham et al, 1981; Keble Martin, 1976) a compromise time of early August was chosen.

Synopsis of field allocation studies

This involved the collection of R. repens plants from three field sites, used for the collection of plants in experiment 3, throughout 1983. Experiment 3 can be seen as a 'transplant garden experiment' (see Chapter 5) relative to the field collections, i.e. the results can be used to differentiate between genotypic and phenotypic differences in the responses to submergence (see Chapter 1).

Methodology for field allocation studies

During Febuary 1983 a 10m x 10m area was marked out in each of the three sites mentioned in Experiment 3 (see Appendix 1). From each of these areas plants were collected at monthly intervals from February 1983 until June 1983 (a July 1983 collection was attempted but stolons were already disintegrating and so clones could no longer be identified).

Initially twenty plants were collected from each site but this was reduced to ten during May and June to reduce collection time. Plants were sampled randomly (using random numbers as grid references) within the marked areas. Collected plants were harvested and weighed as in Experiment 1.

2.4.2 Ranunculus sceleratus experiments

Synopsis of Experiment 4

This experiment was designed to study the effects of seedling submergence on future flowering and allocation patterns. The influence of nutrient level on the response to submergence was also investigated.

Methodology for Experiment 4

During Febuary 1983 seeds of R. sceleratus (the seeds were collected in August 1982 and stored at 5°C) were sown onto John Innes no 1 compost and left to germinate in the greenhouse; the temperature was maintained above 5°C by the use of a thermostatically controlled heater. Throughout the experiment a 16 hour photoperiod was maintained, natural

light being supplemented by a bank of three Thorn PAR mercury vapour lamps (this was to ensure that photoperiod was long enough to allow R. sceleratus plants to flower as some have been shown to be Long Day plants (Samarakoon and Horton, 1981).

After 17 days 30 two-leaved seedlings (i.e. cotyledons only) were transplanted individually into 15cm plastic pots containing John Innes no. 1, 2 or 3 compost (Table 2.2) to give ten seedlings per compost type. After 4 days five seedlings from each compost type were placed into a tank (80 x 40 x 30cm) and submerged with water to a depth of 8cm above the soil surface. The other five seedlings from each compost type were left as controls with soil moisture being maintained by a sand table. After 7 days the water level was lowered in the tanks and the submerged plants were placed on to the sand table with the control plants. The pots were then randomly placed within a 6 x 5 grid to minimize differences in the micro-climate due to position.

The dates of flowering stem elongation, first flowering, and seed production were recorded. During seed production, seed heads were counted and the seed collected. Maximum flowering stem height was also recorded. After seed production had finished the plants were harvested and divided into root, leaves, flowering stem, receptacles and seed. (Initially it was decided to separate the basal rosette leaves from the flowering stem leaves but differences in the morphology of submerged and control plants resulted in these categories being merged into one for all leaves). Weighing and drying details were as in experiment 1.

The date of harvest was chosen to be at the end of seed production. The end of seed production was decided with the help of information from preliminary studies on the floral biology of R. sceleratus. These

Table 2.2

'Available' nutrients and pH analyses** of John Innes composts used in experiment 4.

John Innes compost	N (mg/l*)	P (mg/l)	K (mg/l)	pH
No. 1	138	42	131	6.5
No. 2	245	40	142	6.5
No. 3	300	54	142	6.6

** Source: ADAS soil analysis.
* per litre of soil dried at 30°C (N as nitrate and all 'available' forms of K and P).

studies showed that R. sceleratus seed production rises gradually to a maximum and then falls off rapidly from this peak. Rapid senescence and death follows this peak so that most plants are dead two weeks after peak seed production. Plants were harvested one week after peak seed production. It was also found that seedling submergence did not alter this pattern of seed production and senescence.

Synopsis of Experiment 5

This experiment led directly from experiment 4 and investigated the changes in dry weight allocation and structure of seedlings during short-term submergence.

Methodology for Experiment 5

Seedlings were obtained by the same method as in experiment 4 (using the same source of seeds) and the greenhouse conditions were also the same. Forty-five seedlings were transplanted individually into 9cm plastic pots containing either John Innes no 1, 2 or 3 (see Table 2.2) to give fifteen seedlings per compost type. After 4 days five seedlings from each compost type were placed into tanks (as in experiment 4) and submerged with water to a depth of 8cm. Five seedlings were placed onto a sand table and the remaining five were harvested. Plants were harvested into root, petiole and hypocotyl, and leaves. Petiole and hypocotyl lengths were also measured.

Synopsis of Experiment 6

This experiment led from the two previous experiments where no plant mortality had been recorded throughout the experiments. It was designed

to study seedling mortality during submergence with a much larger number of seedlings.

Methodology for Experiment 6

Again seedlings were obtained by the method given in experiment 4 and greenhouse conditions were the same. One hundred and eighty seedlings were transplanted into 9cm plastic pots containing John Innes 1, 2 or 3 to give sixty seedlings per compost type. After 4 days thirty seedlings from each compost type were submerged as in experiment 5, the remaining thirty from each compost type being placed onto the sand table. After 1 week seedling mortality/survival was recorded.

Synopsis of Experiment 7

This experiment, unlike previous experiments, investigated the response of R. sceleratus to long term submergence. Again plants were initially submerged as seedlings.

Methodology for Experiment 7

Seedlings were obtained by the usual method (experiment 4) and greenhouse condition were also the same. After three weeks seedlings with 3 or 4 leaves (including the cotyledons) were transferred into 15cm pots containing a 50:50 mixture of John Innes no. 2 and Levingtons potting compost.

After three days three plants were then placed into a small tank (20 x 45 x 25cm) and the plants submerged to a depth of 8cm above the soil surface. Another three plants were left on a sand table to act as

controls.

The production of flowers and seed was monitored until all the plants died. Ripe seed heads were collected when necessary, but summed to give weekly totals. Flowering stem height was also measured.

Synopsis of Experiment 8

This experiment investigated the ability of R. sceleratus seeds to germinate underwater.

Methodology for Experiment 8

Seeds of R. sceleratus were sown at a depth of 3mm into seed trays (12 x 7 x 3cm) containing John Innes no. 2. (Unlike other experiments the seeds were buried because surface sown seeds float; a depth of 3mm was found to reduce loss of seed through flotation to acceptable levels). Fifty seeds were sown into each of eight trays on a 1cm x 1cm grid. Four trays were then placed into tanks (as experiment 4) and submerged with water to a depth of 8cm above the soil surface; the other four trays were placed onto a sand table to keep the compost moist. Seedling emergence was monitored on a daily basis for two months.

Synopsis of Experiment 9

This series of experiments was designed to study the effects of diurnally fluctuating temperatures on seed germination in R. sceleratus. The seeds used in this experient were collected fresh from the Port Meadow site during June 1983. For the second part of the experiment these seeds had been stored at 5°C for four weeks.

Methodology for Experiment 9

Seeds of R. sceleratus were placed onto strips of filter paper which were kept moist. This was achieved by placing both ends of each strip in a reservoir of water and supporting the central piece above the water using a glass platform. The whole arrangement was enclosed in a 5cm daimeter petri-dish.

Fifty seeds were placed into each petri-dish and ten petri-dishes were used in each treatment. The treatments took place under a 12 hour photoperiod in a controlled environment chamber (Warren-Sherer) with light being provided by a mixture of fluorescent tubes and tungsten filament bulbs to give a mean irradiance of $60Wm^{-2}$.

Two temperature treatments were used. Firstly seed germination at a constant 20°C was tested and secondly germination in a 25°C (light)/15°C (dark) treatment. Seed germination (scored by possession of a visible radicle) was followed on a daily basis for 4 weeks.

Synopsis of demographic studies on R. sceleratus

In contrast to R. repens very little information about the demography of this species is available. The site for this study was a ditch on the edge of Port Meadow, Oxford (see Appendix 2). This study took place from November 1982 until August 1984.

Methodology for demographic studies

A detailed description of the Port Meadow ditch site is given in Appendix 2. During October 1982 three 5m transects, 1m apart, were set

up running down the bank perpendicular to the ditch. Each 5m transect was divided into ten 0.5m x 0.5m quadrats; giving a total of thirty 0.25m^2 quadrats. From right to left (facing the ditch) these transects will be referred to as A, B and C and the individual quadrats referred to as 1 to 10 numbering down the slope (i.e. A1 is the uppermost quadrat of the right-hand transect). Quadrat positions were permanently marked by inserting vertically, at each corner, a piece of PVC tube (3cm diameter and 15cm long) so as to leave 0.5cm of tubing above the surface.

The positions of any R. sceleratus plants within the quadrats were mapped onto A4 pieces of tracing paper using a pantograph (Telsar). The pantograph was set on a small table (40cm x 40cm top and 22cm high). The mapping point of the pantograph was extended (downwards) to give about a 3cm clearance from the soil surface. Because the ground was uneven a small spirit level was attached to the mapping arm of the pantograph; this enabled it to be kept in a level position during mapping.

Mapping was carried out at approximately 14 day intervals from the 3rd December 1982 until the 4th August 1984, amounting to 41 visits. At each visit the diameter (or diameter class) of each rosette or seedling was recorded and, if flowering, flowering stem height and the number of ripe seed heads were also recorded. Ripe seed heads were clipped off once counted; three heads from each flowering plant were retained and the number of seeds per seed head recorded.

At each visit the percentage plant cover of each quadrat was visually estimated to the nearest 5%. Water level was recorded in terms of its position along each transect. The presence or absence of a seed bank

was assessed at five intervals during the study. This involved taking three soil samples (5cm x 5cm x 3cm) at each of three positions down the bank. These were on a level with quadrats 1, 5 and 9 (on one occasion an additional sample was taken on a level with quadrat 10) and were a few metres to the right of the transects. These soil samples were transferred into trays and placed on a sand table in a greenhouse (conditions as experiment 4). The emergence of R. sceleratus seedlings was recorded during a sixty day period, the samples being turned after thirty days.

The transects were surveyed during Spring 1983 (Appendix 2 for method). Maximum and minimum temperatures, and rainfall measurements were obtained for the area for the period of the study from the Meteorological station at Oxford (see Appendix 2).

The results of this work and their discussion have been compiled into several chapters based on key topics and not divided by experiment.

2.5 Statistical procedures

Procedures for t-test, analysis of variance (anova) and chi-squared test were used as given by Campbell (1974). Where necessary the normality of the sample distribution was tested using the Bartlett's and the Kolmogorov-Smirnov tests (Campbell, 1974:200). Within-anova t-tests, using pooled standard errors, were conducted using the procedure given by Mead and Curnow (1983). This latter procedure allows for a more reliable pair-wise comparison of means.

2.6 Allocation data

It is the **relative** dry weights of plant components which are important when studying dry weight allocation. Differences in the total dry weights of plants must be taken into account before comparisons can begin (although the fact that some plants are larger than others is itself interesting). These dry weight differences are usually accounted for by the use of fractions, where organ weight is expressed as a fraction of the total dry weight. These fractions are usually converted into percentages.

Problems with this technique of allocation analysis were encountered when studying the dry weight data for R. repens obtained from the field. Dry weight allocations expressed as percentages were very variable, for example, with stolons (Figure 2.1). The data show an increase in percentage stolon dry weight with increased total dry weight (Figure 2.1). However, when the actual dry weights of stolons are plotted against total dry weights of the plant (clone of attached ramets) there is a very close relationship between stolon dry weight and total dry weight (Figure 2.2). The regression line explains 96% of the variance in the data.

Why do the two models of stolon allocation differ so dramatically? It can be explained mathematically by considering the graph of stolon dry weight (y) plotted against total dry weight (x) (Figure 2.2). The straight line relationship of stolon dry weight with total dry weight can be expressed as:

$$y = mx + c \qquad \text{---------- 1}$$

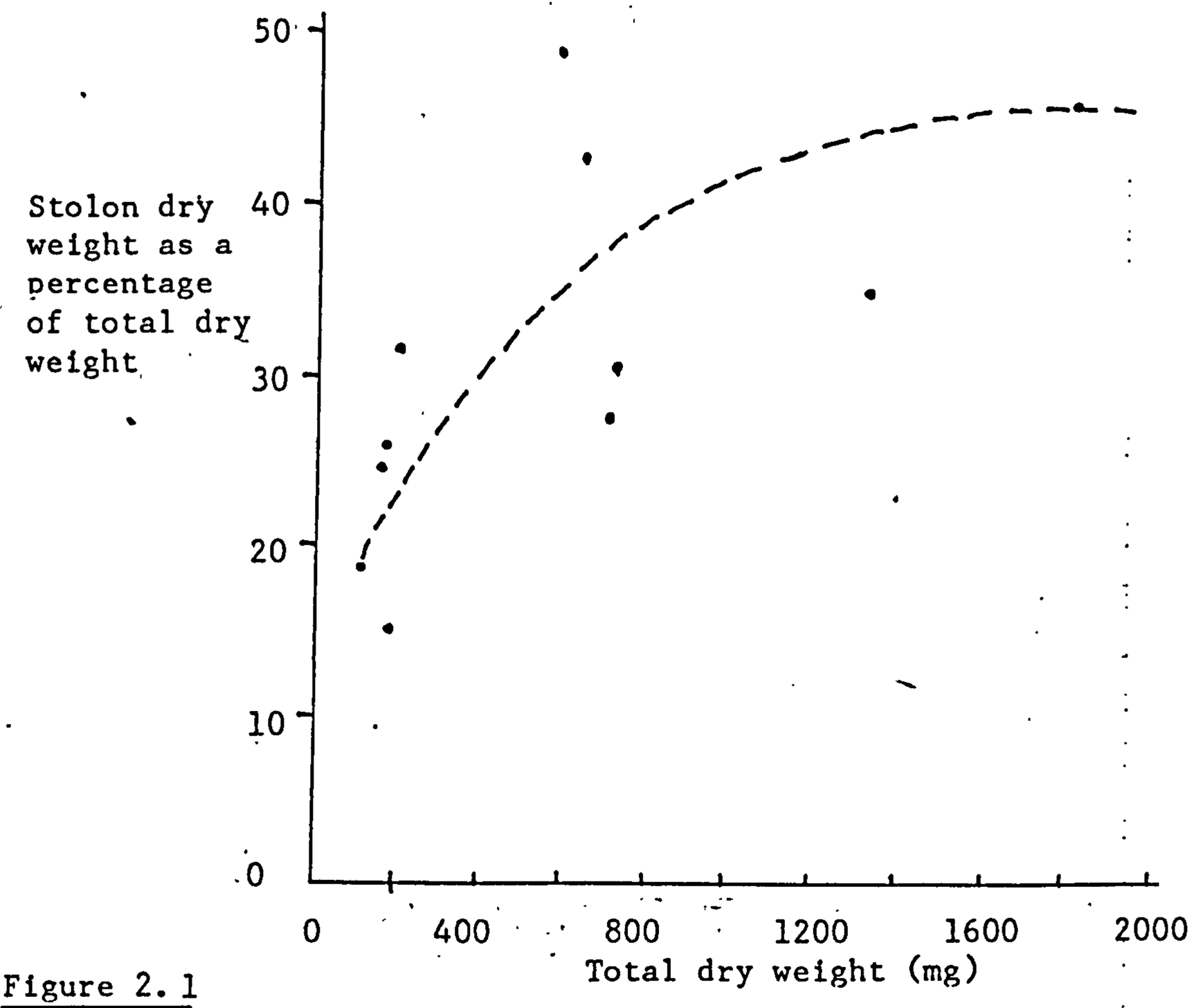


Figure 2.1

Stolon dry weight as a percentage of total dry weight plotted against total dry weight for R. repens plants (plants from Port Meadow-June 1983).

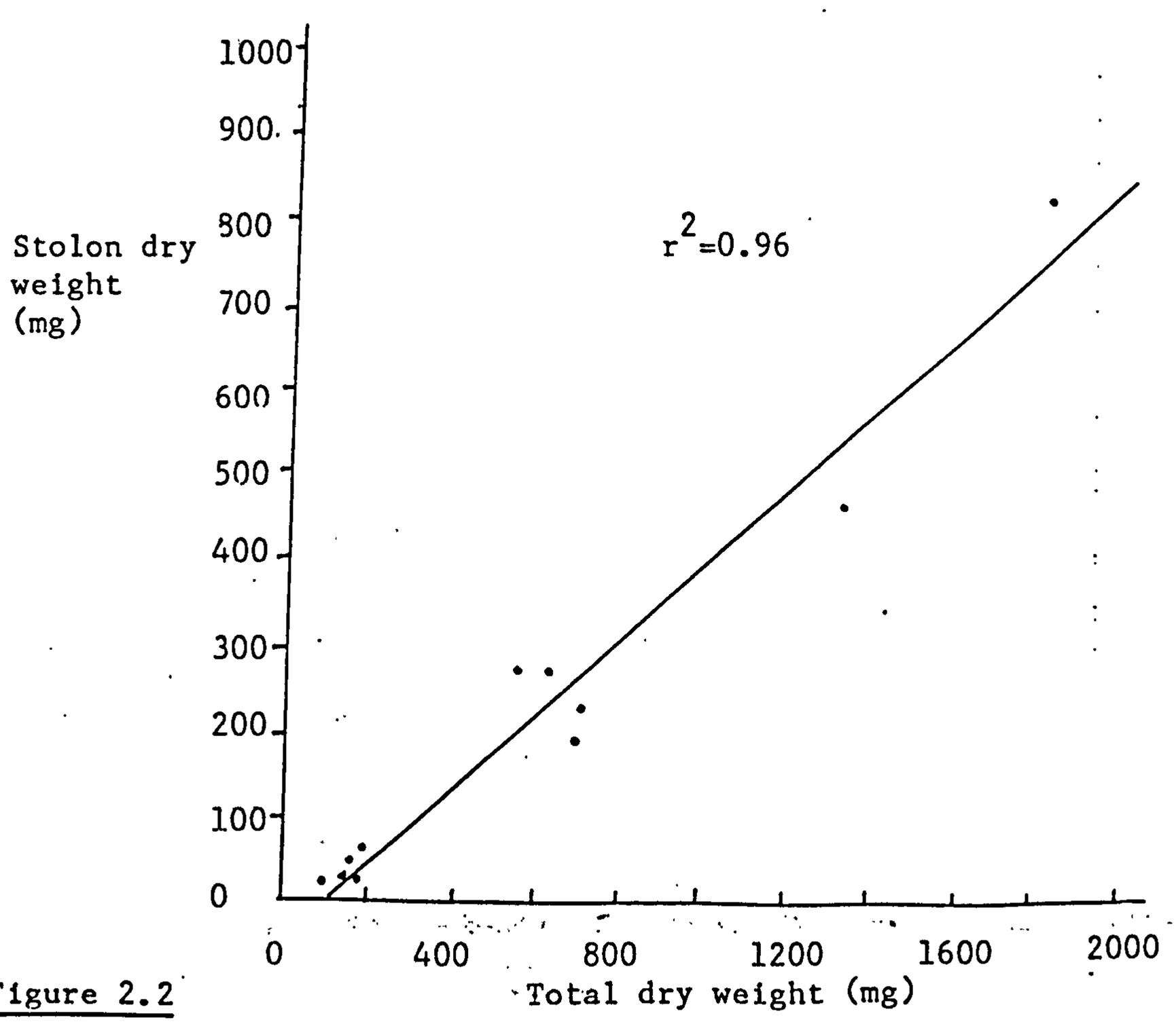


Figure 2.2

Stolon dry weight plotted against total dry weight for R. repens plants (same plants as in Figure 2.1).

where y = stolon dry weight; x = total dry weight; m = gradient of line and c = y-axis intercept.

The gradient, m is constant which implies a constancy of dry weight allocation to stolons independent of total dry weight. This 'slope allocation' can be expressed by rearranging equation 1:

$$\text{Slope allocation} = m = (y-c)/x \quad \text{---------- 2}$$

The usual 'fractional allocation' calculation can be expressed as:

$$\text{Fractional allocation} = y/x \quad \text{---------- 3}$$

Equation 3 is equivalent to equation 2 when c = 0. In other words, the traditional method of calculating allocation has a built-in assumption that c = 0. This is not the case for the results obtained with R. repens shown here (Figures 2.2 & 2.3) and, in fact, in none of the relationships between organ dry weight and total dry weight for field and pot-grown plants was c = 0. For large values of y and x the assumption that c = 0 has a lesser effect. This is because the value of c in the term 'y-c' becomes insignificant compared to y. This explains the increase, and subsequent levelling off, of fractional allocation with increasing total dry weight (Figure 2.1).

The 'slope allocation' method of allocation analysis was found to be similarly effective for the transplant garden data (Figure 2.3) and will be the source of allocation data unless otherwise stated.

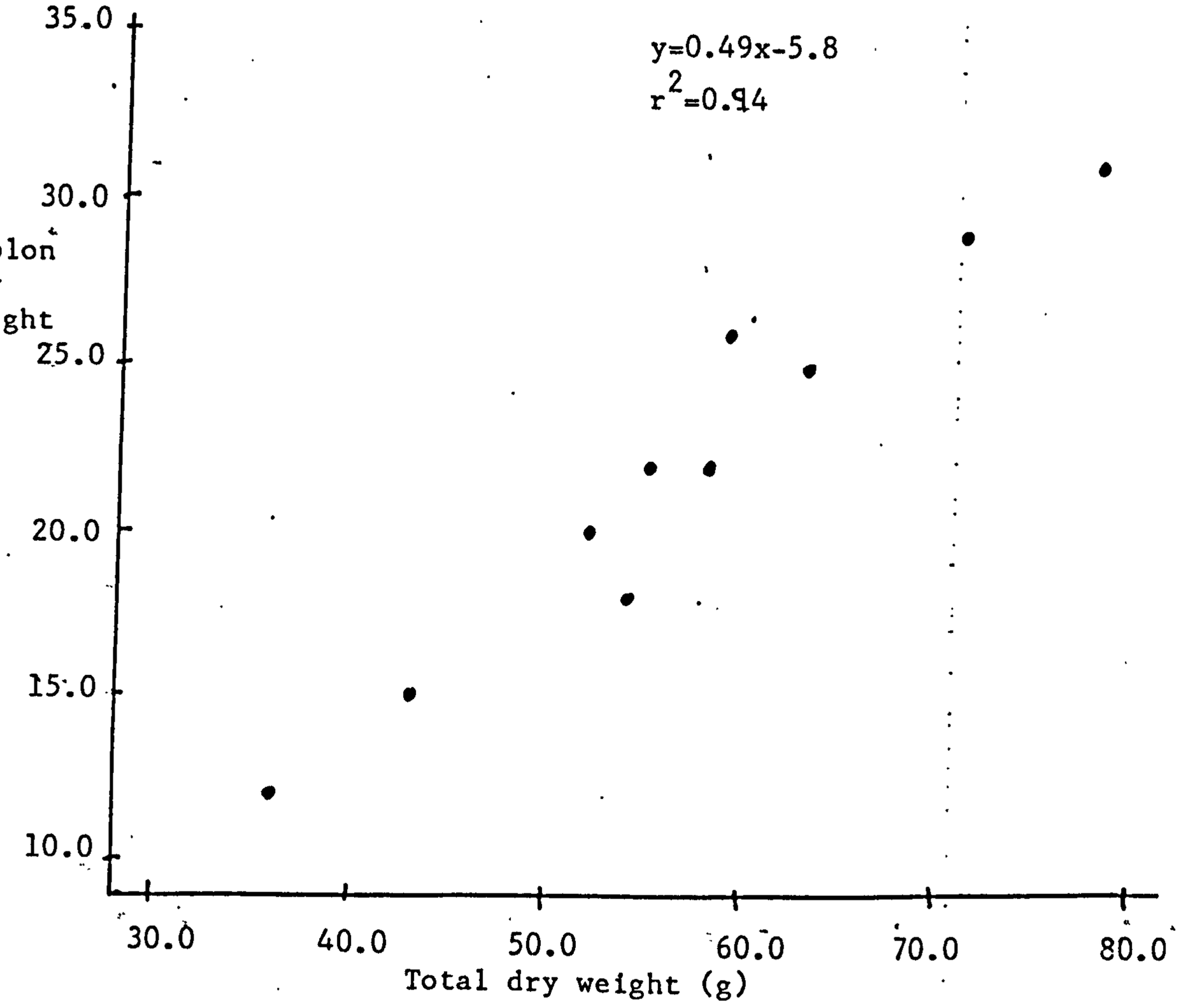


Figure 2.3

Stolon dry weight plotted against total dry weight for pot grown R. repens plants in experiment 3 (see section 2.5).

Evidence for the applicability of the above findings to other plants has been found in data given in Reinartz (1984b) working with Verbascum thapsus. He found a positive correlation between percentage dry weight allocation to seeds with total dry weight weight (Figure 2.4) similar to the one found with stolons in this study (Figure 2.1). However, he did not replot his data in terms of actual dry weights as was done in this study. When this is done the same result as with stolons in this study is found, that a straight line relationship between seed dry weight and total dry weight exists (Figure 2.5).

This shows a constant slope allocation above a base-line dry weight. The regression explains 97.3% of variance in the data, compared with 68.9% in the regression of the percentage data. The two models differ in their predictions of the seed weight of, for example, a plant with a total dry weight of 200g. The percentage model predicts a seed weight of 19.3g, whereas the slope allocation model predicts a seed weight of 15.3g. The greater the total dry weight the greater the discrepancy in the values predicted by the two models.

Further work is required to judge the universal use of the slope allocation model. However, Waite and Hutchings (1982) working on Plantago coronopus found that perecentage allocation to seed increased with total dry weight and that there was a straight line relationship between seed dry weight and total dry weight (Figure 2.6). This presents a similar picture to the results in this study.

Bradbury and Hofstra (1976) found that percentage allocation data, based on dry weights converted to calories, implied that the allocation patterns of two populations of Solidago canadensis were, in some respects, significantly different. However, when the results were

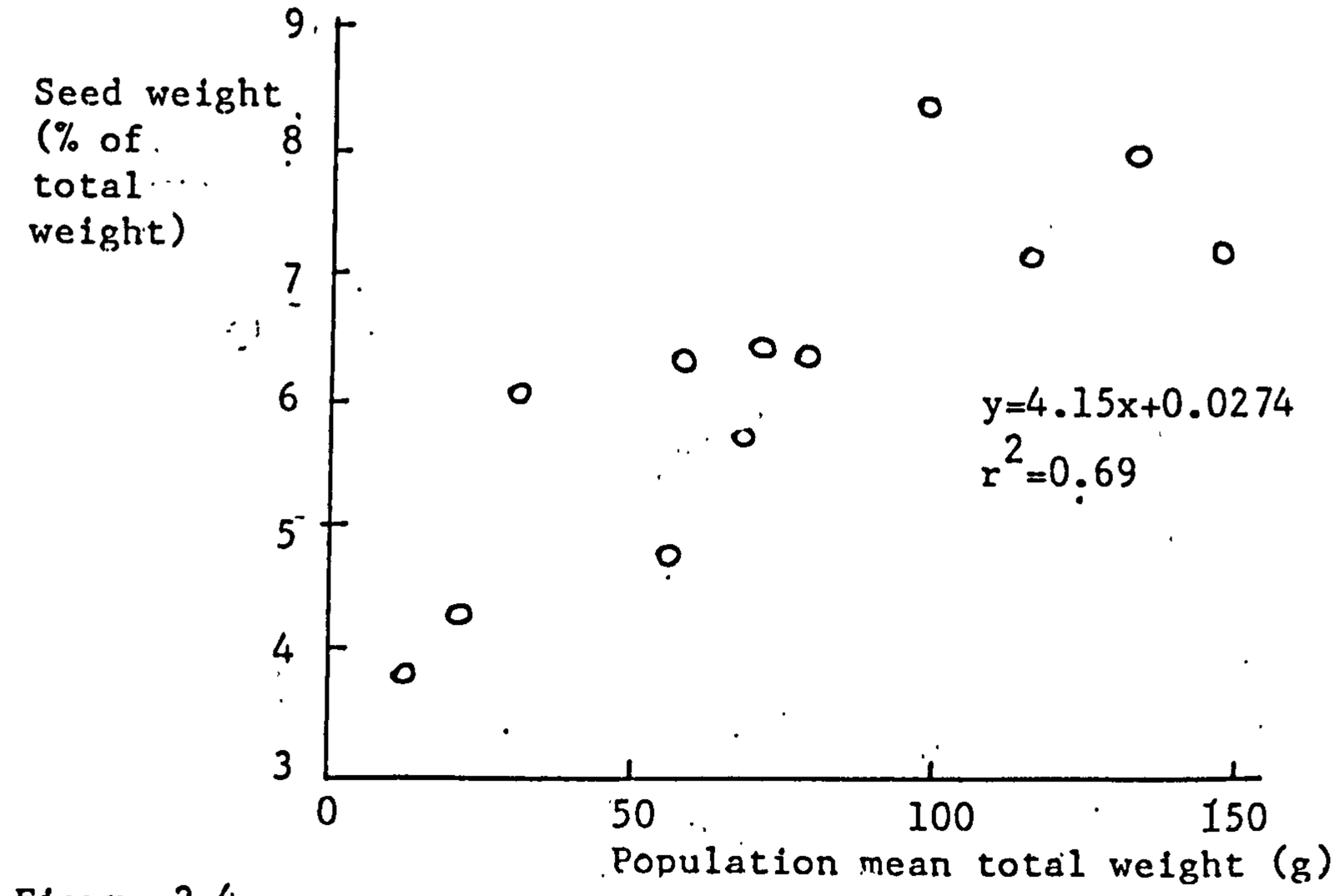


Figure 2.4

Dry weight of seeds as a percentage of total dry weight plotted against total dry weight for Verbascum thapsus plants from North America (from Reinartz, 1984b).

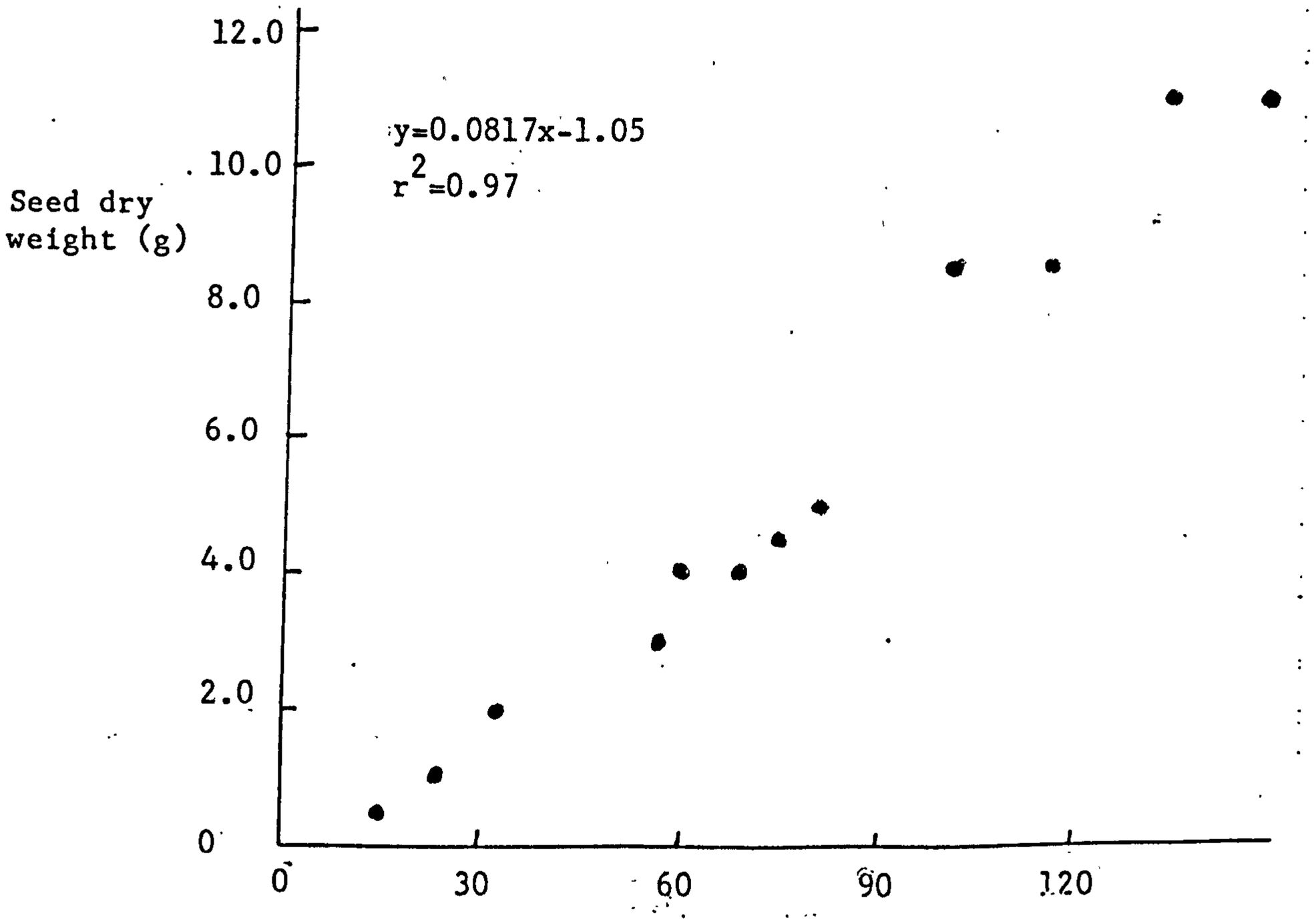


Figure 2.5

Dry weight of seeds plotted against total dry weight for the Verbascum thapsus plants in Figure 2.4 (data from Reinartz, 1984b).

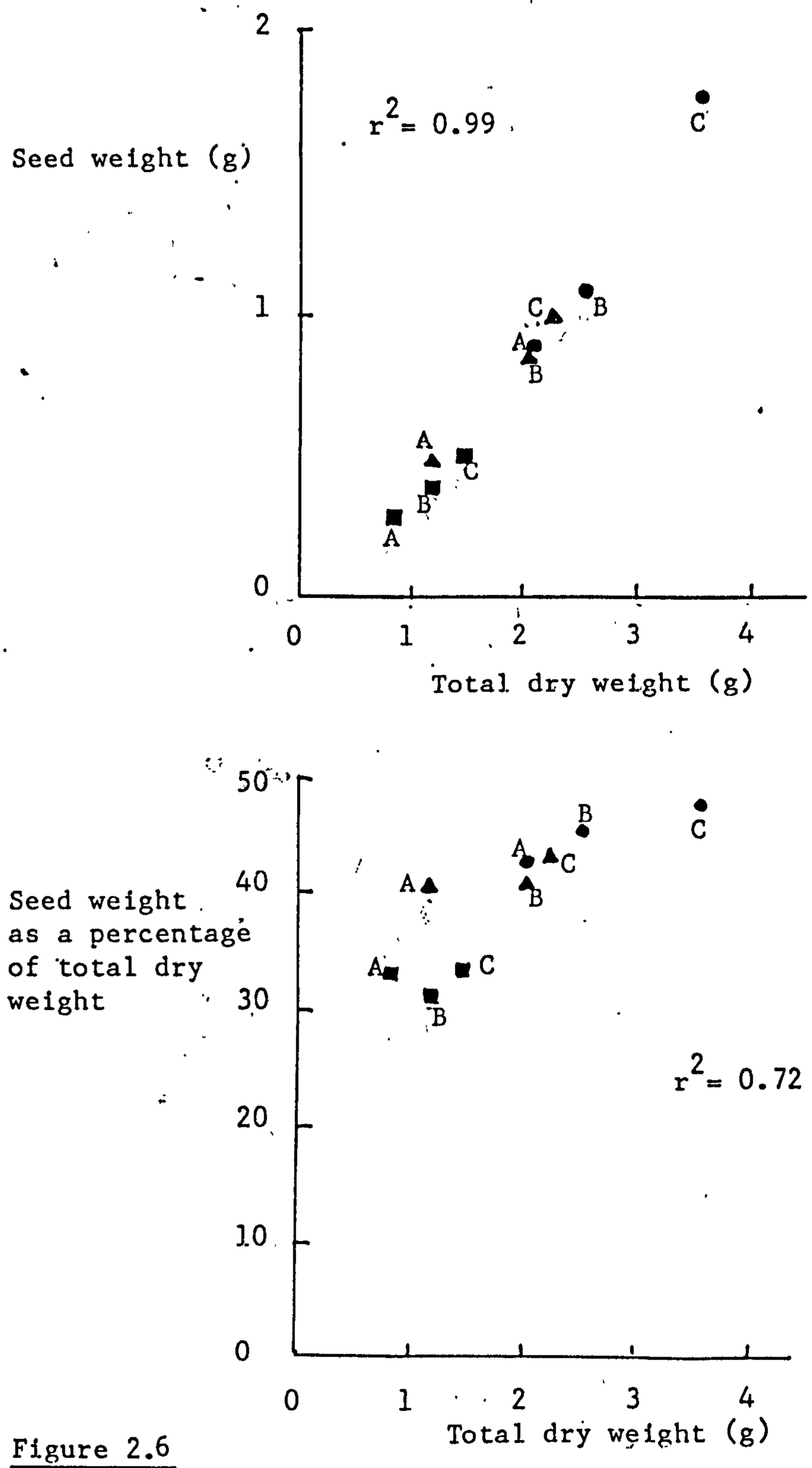


Figure 2.6

(a) Dry weight of seeds plotted against total dry weight for Plantago coronopus plants (from Waite and Hutchings, 1982).

(b) Dry weight of seeds as a percentage of total dry weight plotted against total dry weight for the same plants as in part (a) (from Waite and Hutchings, 1982).

(letters and symbols on graphs refer to different treatments and sites of origin of plants).

plotted as actual calorie content of the component parts against actual total calorie content of the plant on a log-log scale, these differences were no longer apparent, the two populations lying on the same (highly significant) regression lines. Bradbury and Hofstra (1976) conclude that '...this apparent anomaly is explicable in terms of plant size...'. In other words percentages did not account for plant size differences as they were intended to do. This is another example of the possible misinterpretation of results from the use of percentages.

2.7 Summary

1. There are several difficult methodological problems relating to the "principle of allocation".

2. Allocation results are very researcher-dependent.

3. Problems with the usual "percentage" allocation system resulted in a change to a novel "slope" allocation model.

Chapter 3

Dry Weight Allocation and Submergence in Ranunculus repens

1. Tactical allocation changes with submergence.

".. most plant resource allocation studies have concentrated on the measure of dry weight distribution among tissues differing in life history function.. "

(Watson, 1984)

3.1 Introduction

This is the first in a series of three Chapters (3, 4 and 5) devoted to the study of dry weight allocation strategies and tactics in R. repens plants in relation to seasonal submergence. This first chapter is concerned with **tactical** changes in allocation associated with submergence whereas Chapter 4 is concerned with allocation patterns under seasonally submerged and non-submerged conditions in the field. The third chapter in this series (Chapter 5) is concerned with genetic differentiation with respect to dry weight allocation patterns between populations of R. repens which have in the past been subject to different levels of seasonal submergence.

The experiments discussed in this chapter were designed, firstly, to study how much of a 'stress' (sensu Grime, 1979) submergence is to R. repens plants; secondly, to quantify tactical changes in dry weight allocation resulting from submergence and to outline a submergence

response strategy based on these allocation changes (see section 1.2); and thirdly, to study any changes in phenology resulting from submergence.

Submergence of R. repens rosettes has been observed, under controlled and field conditions, to result in the elongation of petioles (Ridge, 1985; Smith pers. obser.). However, the plants also appear smaller (Smith pers. obser.). The following questions are of immediate interest:

1. Are submerged plants smaller in terms of dry weight?

2. Do the observed changes in structure involve changes in dry weight allocation?

3. Can any changes in flowering and/or stolon production be identified?

4. Can a 'stress response strategy' (see section 1.8) for submergence be outlined?

3.2 Experimental Results

3.2.1 Experiment 1

Experiment 1 involved three treatments: 13 weeks air grown (controls); 5 weeks submergence followed by 8 weeks air grown; and 13 weeks continuous submergence (details in section 2.4). Time-zero control plants were harvested at the start of the experiment. Plants from the Open University site were used in this experiment (see Appendix 1).

Plants in both submergence treatments had lower total dry weights than the control plants (Table 3.1) but the 13 week submerged plants show a much greater reduction. During the last two weeks of the experiment the leaves of one of the 13 week submerged plants ('plant V') reached the surface of the water and achieved a dry weight twelve times that of the other submerged plants (Table 3.1). Plant V was excluded from the analysis of the 13 week submerged plants but where possible included solely for reference (Table 3.1). The total dry weights of the time-zero plants show that the 13 week submerged plants had a net loss of dry weight (Table 3.1).

This loss of dry weight gives the 13 week submerged plants a negative relative growth rate (RGR; see Larcher, 1980) (Table 3.2). Plant V shows a virtually zero RGR (Table 3.2) but this is averaged over the whole 13 weeks, the RGR for the final two weeks would have been much greater. The RGR for the 5 weeks submerged plants is roughly half that of the controls (Table 3.2).

None of the 13 week submerged plants produced stolons during the experiment but two of the 5 week submerged plants and seven of the control plants did produce stolons (Table 3.3). Only plants in the control treatment produced any daughter ramets (Table 3.3).

The dry weight of component parts was reduced by submergence (Table 3.4) and this reduction was greatest in the 13 week submerged plants. Allocation of dry weight to components (based on the graphical technique discussed in section 2.6) shows a more complex picture (Table 3.5). Overall there is a trend with submergence to increased allocation to underground structures and petioles, and decreased allocation to leaves, stolons and ramets (Table 3.5).

Table 3.1

Total dry weights (mean and S.E.) for *R. repens* plants grown in experiment 1.

Treatment	Total dry weights (mg)	n
Controls	1618.4 (161.9)a**	12
5-week submerged	947.4 (95.0)b	12
13-week submerged	10.2 (0.9)c	11
"Plant V"	123.0 n/a	1
Time-zero controls	122.1 (5.4)d	6

** as in all tables different superscript indicates significantly different at $p<0.05$ (pair-wise t-test).

Table 3.2

Relative growth rates (RGRs, means) for *R. repens* plants grown in experiment 1.

Treatment	RGRs (mg/mg/week)
Controls	0.943
5-week submerged	0.520
13-week submerged	-0.070
"Plant V"	0.001

Table 3.3

Number of *R. repens* plants in experiment 1 producing stolons and ramets.

Treatment	Stolons	Ramets	n
Controls	7	7	12
5-week submerged	2	0	12
13-week submerged	0	0	11
"Plant V"	0	0	1
Time-zero controls	0	0	6

Table 3.4

Dry weights (mean and S.E.) of component organs for R. repens plants in experiment 1 (n as Table 3.2).

Treatment	Dry weights (mg)				
	Leaves	Petioles	Underground	Stolons	Ramets
Controls	488.9 (42.1)[a]	277.8 (26.0)[a]	740.7 (94.5)[a]	72.8 (21.5)[a]	38.3 (13.0)[a]
5-week submerged	265.4 (27.5)[b]	161.6 (16.2)[b]	516.5 (59.9)[b]	4.0 (3.8)[b]	0[b]
13-week submerged	1.1 (0.1)[c]	3.1 (0.2)[c]	5.9 (0.5)[c]	0[c]	0[b]
"Plant V"	33.0	61.0	31.0	0	0
Time-zero controls	30.5 (1.2)[d]	23.7 (1.9)[d]	68.0 (2.7)[d]	0[c]	0[b]

Table 3.5

Dry weight allocation (mean and S.E.) to component organs based on the slope allocation method (section 2.6) in R. repens plants grown in experiment 1 (n as Table 3.2).

Treatment	Dry weight allocations				
	Leaves	Petioles	Underground	Stolons	Ramets
Controls	0.251 (0.006)[a]	0.124 (0.009)[a]	0.555 (0.010)[a]	0.051 (0.011)[a]	0.019 (0.007)[a]
5-week submerged	0.261 (0.009)[a]	0.146 (0.007)[a]	0.598 (0.008)[b]	0.004 (0.004)[b]	0[b]
13-week submerged	0.138 (0.003)[b]	0.239 (0.003)[b]	0.623 (0.004)[c]	0[b]	0[b]
Time-zero controls	0.218 (0.002)[a]	0.310 (0.036)[b]	0.472 (0.036)[a]	0[b]	0[b]

However, the control and 5 week submerged plants do not differ significantly in their allocations to petioles or leaves. The 13 week submerged plants show a very different pattern of allocation compared to the other treatments (Table 3.5). The time-zero plants show a relatively high allocation to petioles (not significantly different from the 13 week submerged plants) but a relatively low allocation to underground structures (not significantly different from controls) and an intermediate level of allocation to leaves (Table 3.5).

The emphasis on allocation of dry weight to petioles relative to leaves in the 13 week submerged plants can also be seen in the petioles:leaves dry weight allocation ratios (Table 3.6). The ratios for the controls and 5 week submerged plants, although similar, reflect a greater emphasis on leaves relative to petioles in the control plants compared to the 5 week submerged plants. However, the 13 week submerged plants show a considerable emphasis on allocation to petioles relative to leaves compared with both the other treatments (Table 3.6). The time-zero plants also show a large emphasis on petiole allocation relative to leaves compared to the control and 5 week submerged plants but not as great as the 13 week submerged plants (Table 3.6).

The emphasis in submerged plants on allocation to underground structures can be seen in the below ground:above ground dry weight allocation ratios (= root:shoot ratio) (Table 3.7). However, unlike the petioles:leaves allocation ratio the 5 week submerged plants are clearly intermediate between the controls and the 13 week submerged plants, reflecting increased emphasis on underground structures relative to above ground structures with increased submergence. The time-zero plants show an even greater emphasis on above ground allocation relative to below ground compared to the control plants (Table 3.7).

Table 3.6

The ratio of dry weight allocation to petioles with dry weight allocation to leaves in R. repens plants grown in experiment 1.

Treatment	Ratio
Controls	0.494
5-week submerged	0.559
13-week submerged	1.732
Time-zero controls	1.422

Table 3.7

The ratio of dry weight allocation to underground structures with allocation to above ground structures in R. repens plants grown in experiment 1.

Treatment	Ratio
Controls	1.25
5-week submerged	1.47
13-week submerged	1.65
Time-zero controls	0.89

3.2.2 Experiment 2

This experiment also involved Open University site plants (see Appendix 1). Three treatments were set up: 12 weeks air grown (controls); 4 weeks submergence followed by 8 weeks air grown; 8 weeks submergence followed by 4 weeks air grown (details in section 2.4).

The 8 week submerged plants suffered substantial mortality (Table 3.8) but there was none in the 4 week submerged plants and only 1 plant in the control treatment died. All plants alive at harvest, independent of treatment, produced stolons but **only** plants in the control treatment flowered (Table 3.8).

The submerged plants showed reduced total dry weight at harvest compared to the controls, with the 8 week submerged plants having the greatest reduction (Table 3.9). All treatments showed positive RGR's (Table 3.10) but the RGR for the 8 week submerged plants was very low. The RGR for the control plants was over three times the RGR for the 4 week submerged plants and nearly fifty-seven times greater than the 8 week submerged plants (Table 3.10).

The dry weights of the individual component organs were also reduced by submergence (Table 3.11), with the 8 week submerged plants showing the greatest reductions relative to the controls. Although the dry weight of stolons fell dramatically in the submerged plants (Table 3.11) dry weight allocations (using the graphical technique discussed in section 2.6) to stolons were unaffected by submergence (Table 3.12).

However, there is a trend for decreased allocation to leaves plus petioles with submergence. The allocation pattern shown by the 4 week

Table 3.8

Survival, and the number of R. repens plants producing stolons and flowers in experiment 2.

Treatment	Initial n	Final n	Stolons	Flowers
Controls	12	11	11	6
4-week submerged	12	12	12	0
8-week submerged	12	6	6	0

Table 3.9

Total dry weights (per plant means and S.E.) for R. repens plants grown in experiment 2.

Treatment	Total dry weight (g)	n
Controls	10.39 (1.51)[a]	11
4-week submerged	3.34 (0.26)[b]	12
8-week submerged	0.33 (0.07)[c]	6
Time-zero controls	0.12 (0.01)[d]	6

Table 3.10

Relative growth rates (per plant mean) for R. repens plants grown in experiment 2 (n as Table 3.9).

Treatment	RGR (g/g/week)
Controls	6.90
4-week submerged	2.16
8-week submerged	0.14

Table 3.11

Dry weights of component organs (g, per plant, mean and S.E.) for R. repens plants grown in experiment 2 (n as Table 3.9).

Treatment	Petioles + Leaves	Underground	Stolons	Ramets
Controls	5.277 (0.832)[a]	2.147 (0.318)[a]	1.431 (0.276)[a]	1.532 (0.208)[a]
4-week submerged	1.553 (0.111)[b]	0.711 (0.049)[b]	0.283 (0.050)[b]	0.797 (0.130)[b]
8-week submerged	0.017 (0.008)[c]	0.178 (0.033)[c]	0.033 (0.011)[c]	0.105 (0.020)[c]
time-zero controls	0.055 (0.003)[d]	0.069 (0.002)[d]	0[d]	0[d]

Table 3.12

Dry weight allocation to component organs (per plant, mean and S.E. based on the graphical technique discussed in section 2.6) for R. repens plants grown in experiment 2 (n as Table 3.9).

Treatment	Petioles + Leaves	Underground	Stolons	Ramets
Controls	0.543 (0.014)[a]	0.204 (0.005)[a]	0.143 (0.011)[a]	0.119 (0.007)[a]
4-week submerged	0.312 (0.027)[b]	0.137 (0.012)[b]	0.156 (0.010)[a]	0.395 (0.029)[b]
8-week submerged	0.110 (0.005)[c]	0.455 (0.015)[c]	0.155 (0.006)[a]	0.280 (0.007)[c]
time-zero controls	0.550 (0.014)[a]	0.450 (0.011)[c]	0[b]	0[d]

submerged plants for ramets and underground structures is not intermediate between the other two treatments (Table 3.12) and so a trend is not evident. The 8 week submerged plants show much greater dry weight allocation to both these components compared to the controls.

The below ground:above ground dry weight allocation ratios (= root:shoot ratio) show that the 8 week submerged plants have increased emphasis on underground structures relative to above ground compared to the other plants (Table 3.13). The 4 week submerged plants show a greater emphasis on above ground allocation than the controls (Table 3.13). The time-zero plants show a greater emphasis on underground structures than the 8 week submerged plants; this is possibly related to the lack of stolons and ramets in these plants.

The stolon:ramet dry weight allocation ratio shows an increased emphasis on allocation to ramets relative to stolon allocation with submergence (Table 3.14). However, it is the 4 week plants that show the greater emphasis on ramets relative to stolons (Table 3.14).

3.3 Discussion

From both experiments it is clear that submergence results in reduced total dry weights (Tables 3.1 & 3.9) and reduced RGR's (Tables 3.2 & 3.10) and that these effects are greater with increased submergence. Following the definition of stress as '...external constraints which limit the rate of dry matter production...' (Grime, 1979; see section 1.8), it is clear that R. repens plants were under stress conditions in the submergence treatments given. There is also evidence of a delay in stolon and ramet production (experiment 1: Table 3.3), and flowering

Table 3.13

Below ground: above ground dry weight allocation ratios (per plant, mean) for R. repens plants grown in experiment 2 (n as Table 3.9).

Treatment	Ratio
Controls	0.256
4-week submerged	0.159
8-week submerged	0.835
time-zero controls	0.818

Table 3.14

Stolons: ramets dry weight allocation ratios (per plant, mean) for R. repens plants grown in experiment 2 (n as Table 3.9).

Treatment	Ratio
Controls	1.202
4-week submerged	0.395
8-week submerged	0.554

(experiment 2: Table 3.8) and also an increase in plant mortality (experiment 2: Table 3.8).

The greater total dry weight of 'plant V' (of experiment 1 - the leaves of which reached the water surface during the last two weeks of the experiment) compared to the other 13 week submerged plants (Table 3.1) points to some of the reduced dry weight of submerged plants being due to the presence of water around the leaves.

Light is unlikely to be limiting in such clear, shallow water (Maberley and Spence, 1983). However, carbon dioxide is present in only very small amounts in freshwater (Maberley and Spence, 1983) and it is unlikely that R. repens is able to use bicarbonate (Allen and Spence, 1981; Raven, 1970). This could be a limiting factor on dry weight gain. This does not rule out the role of soil hypoxia (or anoxia) in the reduction of dry weight through either the reduction of nutrient availability (Gambrell and Patrick, 1978) and/or the increased metabolic activity associated with the de-toxification of the products of anaerobic metabolism (see section 1.7).

Increased emphasis on below ground structures in submerged plants is clear from the increased allocation to these structures and the increased 'root:shoot' allocation ratios with increased submergence in experiment 1 (Tables 3.5 & 3.7). In experiment 2 this emphasis in allocation is shown by the 8 week submerged plants having a much greater allocation to underground structures than the controls but the 4 week plants do not show this pattern (Table 3.12). The 'root:shoot' ratios also show that the 4 week submerged plants are not intermediate between controls and 8 weeks submerged plants (Table 3.13). These results suggest that the submergence periods are not additive in their effects

on allocation.

Increases in the 'root:shoot' ratios of plants in 'stressful' environments are well documented (Fitter and Hay, 1981:102; Waite and Hutchings, 1982). In this situation these could be considered to be associated with the need for increased nutrient absorption but Fitter and Hay (1981:103) state '... the root:shoot ratio is ... a good guide to the stressfulness of the environment but bears little relation to nutrient absorption ...'. They base this statement on the frequent finding that increased root:shoot ratios in stressful environments are due to increased allocation to subterranean storage organs.

However, the R. repens plants in these experiments often showed a total absence of storage organs (caudex and rhizome) after growing under submerged conditions (S.J. Smith pers. obser.). Plants growing in the field under submerged conditions also showed reduced underground storage organs compared to non-submerged plants (S.J. Smith, pers. obser.). It may be that the increase in root:shoot in R. repens under submerged conditions is in response to nutrient deficiency as found by Bradshaw et al (1964) for several grasses.

The dry weight allocation to leaves and petioles, and the petioles :leaves dry weight allocation ratio of the plants in experiment 1 (Tables 3.5 & 3.6) show an increased emphasis on petioles relative to leaves. This emphasis on petioles in submerged plants may be related not only to the depth accommodation response of petioles (see Chapter 1) but also to the inability of leaves to develop their full lamina underwater. Plant V shows that long petioles that enable leaves to reach the surface can result in considerable resource gain (Table 3.1).

The submerged plants in experiment 2 show an increased emphasis on ramets relative to stolons. This can be seen in the stolons:ramet dry weight allocation ratios (Table 3.14) and also in the dry weight allocation to ramets and stolons (Table 3.12). The constant allocation to stolons (in experiment 2) suggests a maintenance of allocation for vegetative spread but the increased allocation to ramets points towards greater investment in the survival of their daughter ramets; ramet mortality has been shown to be size related in many clonal perennials (Pitelka, et al, 1985).

3.4 Summary

The submergence treatments resulted in:

1. reductions in dry weight gain.

2. delay or reduction of flowering and in experiment 1 a delay or reduction in stolon production.

3. increased allocation to petioles and underground structures.

4. increased emphasis on ramet relative to stolons.

Chapter 4

Dry Weight Allocation and Submergence in Ranunculus repens.

2. Dry weight allocation patterns in field populations.

"Every plant is a measure of the conditions under which it grows."

(Clements, 1920)

4.1 Introduction

In the previous chapter the dry weight allocation of R. repens plants grown in submerged and non-submerged treatments under controlled conditions was investigated. However, the plants used were from one particular site (see section 3.2) and the conditions were far from those in the field.

This chapter reports the results of dry weight allocation studies carried out upon R. repens plants under field conditions. Two of the chosen sites were on Port Meadow, Oxford. Although adjacent the two sites have very different histories of submergence. One of the sites (the "Port Meadow submerged site") is regularly submerged during the winter and spring, whilst the nearby site (the "Port Meadow non-submerged site") is only very rarely submerged because it is on a higher level. A third site (the "Open University site") is situated on the Open University campus, Milton Keynes and is about 40 miles from Port Meadow. This latter site is on heavy clay soil and is often waterlogged during the winter but submergence is rare (details of these sites are in

Appendix 1).

Three questions were of interest in this study:

1. Do dry weight allocation patterns differ between submerged and non-submerged plants under field conditions?

2. Are the allocation patterns of plants from the two distant non-submerged sites more alike than those of the two Port Meadow sites?

3. How do these differences in allocation pattern (if any) compare with those found under controlled conditions (Chapter 3)?

The field dry weight allocation results can not immediately be used in a discussion of strategies because the genetic component of the response to, for example, submergence has not been assessed (see section 1.2). Several studies have shown adjacent populations of the same plant species to be genetically distinct (e.g. Antonovics, 1972; Aston and Bradshaw, 1966; Turkington, 1979; Lovett Doust, 1981a; 1981b) whilst other studies have shown field differences in allocation patterns to disappear under a common environment (e.g. Hickman, 1975; Abrahamson and Hershey, 1977; Holler and Abrahamson, 1977; Raynal, 1979). The environmental and genetic components of the response to submergence of the plants from the three sites will be investigated in Chapter 5.

4.2 Field Results

There is a considerable range in total genet (this refers to a single rosette with its attached ramets) dry weight within the three sites (Table 4.1). Plants from both Port Meadow sites show a trend of increasing mean total genet dry weight throughout the study period (Table 4.2). However, the Port Meadow non-submerged site plants show a peak in May and June, whereas the Port Meadow submerged site plants show a peak in June (Table 4.2). With the exception of June the Port Meadow submerged site plants were significantly lighter than those of the Port Meadow non-submerged site (Table 4.2).

Plants from both Port Meadow sites show no significant change in dry weight from February to March and about a 2.5 times increase from March to April (Table 4.2). However, from April to May the Port Meadow non-submerged site plants show a doubling of total genet weight but the Port Meadow submerged plants showed no significant change in dry weight. The two sites also differ in the pattern of change from May to June with the Port Meadow submerged site plants showing a large increase in total dry weight and the Port Meadow non-submerged site plants showing no significant change (Table 4.2).

The limited data from the Open University site plants means that a pattern for the whole study period can not be seen (Table 4.2). The February and March data show that the Open University genets were relatively large compared to the Port Meadow plants (Table 4.2). The June data, however, suggests that total dry weight has peaked in the preceding months.

With the exception of the June results organ dry weights are usually

Table 4.1

Range of total plant dry weights (mg) for *R. repens* plants collected from the three field sites February to June 1983.

Month	Site		
	Port Meadow submerged	Port Meadow non-submerged	Open University
February	26-149	95-353	249-777
March	50-278	51-576	174-888
April	97-570	123-1199	n/a
May	80-489	471-1842	n/a
June	399-1766	102-1814	236-809

n/a= no data collection.

Table 4.2

Total plant dry weights (mg, mean and S.E., per plant) for *R. repens* plants collected from the three field sites February to June 1983.

Month	Site			
	Port Meadow submerged	Port Meadow non-submerged	Open University	n
February	84 (7)^{a**}	204 (16)^{b}	424 (36)^{de}	20
March	107 (13)^{a}	189 (32)^{b}	323 (50)^{cd}	20
April	286 (32)^{c}	467 (61)^{de}	n/a	20
May	246 (48)^{bc}	912 (140)^{f}	n/a	10
June	805 (121)^{f}	594 (174)^{ef}	489 (47)^{e}	10

n/a= no data collection.

** different superscript means significantly different at $p<0.05$ (t-test).

greater in the Port Meadow non-submerged site plants compared with the plants from the Port Meadow submerged site (Table 4.3). The February and March data for the Open University site plants show that these plants usually have greater organ dry weights than plants from both Port Meadow sites (Table 4.3).

Dry weight allocation (based on the graphical technique discussed in section 2.6) to parent rosette underground structures shows a declining trend through the study period in plants from both Port Meadow sites (Table 4.4c). From February to April the Port Meadow submerged site plants had a greater allocation to underground structures compared with Port Meadow non-submerged site plants but the situation was reversed in June (Table 4.4c). The Open University site plants shows a tendency to increase underground allocation, but without the April and May data it is difficult to be certain; even so the allocation to these structures in these plants in June is very high relative to the Port Meadow site plants (Table 4.4c).

Allocation to parent rosette leaves in the Port Meadow non-submerged site plants peaked in April and then decreased to below the February levels (Table 4.4a). The Port Meadow submerged site plants show a similar picture but the peak was a month later. Port Meadow non-submerged site plants often show greater allocation to parent rosette leaves compared to the Port Meadow submerged site plants (Table 4.4a). Open University plants often show greater allocation to these components compared to the other site plants.

Allocation to parent rosette petioles does not show as clear a picture as the allocation to leaves (Table 4.4b). Plants from both Port Meadow sites show peaks in allocation, which correspond with the peaks in

Table 4.3

Organ dry weights (mg, mean and S.E., per plant) for R. repens plants collected from the three field sites February to June 1983 (n as Table 4.2)

(a) Parent rosette leaves

Month	Site		
	Port Meadow submerged	Port Meadow non-submerged	Open University
February	5 (1)a	50 (5)b	185 (17)c
March	21 (3)a	45 (8)b	144 (19)c
April	76 (10)a	188 (26)b	n/a
May	85 (19)a	285 (45)b	n/a
June	43 (10)a	56 (18)a	31 (8)a

n/a= no data collection.
** different superscript means significantly different at p<0.05 (t-test) (**rows** only)

(b) Parent rosette petioles

Month	Site		
	Port Meadow submerged	Port Meadow non-submerged	Open University
February	20 (2)a	45 (4)b	106 (9)c
March	29 (3)a	41 (6)b	79 (12)c
April	93 (10)a	107 (17)a	n/a
May	76 (16)a	188 (28)b	n/a
June	74 (20)a	43 (15)a	44 (9)a

(c) Parent rosette underground structures

Month	Site		
	Port Meadow submerged	Port Meadow non-submerged	Open University
February	58 (5)a	109 (10)b	133 (12)b
March	58 (9)a	103 (19)b	99 (19)b
April	117 (15)a	172 (20)b	n/a
May	82 (16)a	314 (46)b	n/a
June	138 (21)a	140 (41)a	141 (21)a

Table 4.3 continued

(d) Stolons

Month	Site		
	Port Meadow submerged	Port Meadow non-submerged	Open University
May	13 (3)[a]	80 (16)[b]	n/a
June	296 (47)[a]	220 (77)[ab]	174 (32)[b]

(e) Ramet leaves

Month	Site		
	Port Meadow submerged	Port Meadow non-submerged	Open University
May	0[a]	23 (3)[b]	n/a
June	79 (15)[a]	52 (20)[a]	47 (5)[a]

(f) Ramet petioles

Month	Site		
	Port Meadow submerged	Port Meadow non-submerged	Open University
May	0[a]	16 (2)[b]	n/a
June	62 (13)[a]	45 (15)[ab]	26 (4)[b]

(g) Ramet underground structures

Month	Site		
	Port Meadow submerged	Port Meadow non-submerged	Open University
June	32 (8)[a]	13 (4)[b]	7 (3)[b]

(h) Floral structures

Month	Site		
	Port Meadow submerged	Port Meadow non-submerged	Open University
May	0[a]	41 (7)[b]	n/a
June	104 (17)[a]	51 (15)[b]	21 (5)[b]

Table 4.4

Dry weights allocation to organs (mean and S.E., per plant - based on graphical technique discussed in section 2.6) for R. repens plants collected from the three field sites February to June 1983.

(a) Parent rosette leaves

Month	Site		
	Port Meadow submerged	Port Meadow non-submerged	Open University
February	0.032 (0.003)a**	0.245 (0.011)e	0.445 (0.011)i
March	0.180 (0.007)d	0.239 (0.004)e	0.384 (0.005)h
April	0.300 (0.005)f	0.428 (0.004)i	n/a
May	0.378 (0.006)h	0.318 (0.005)g	n/a
June	0.074 (0.005)b	0.109 (0.011)c	0.119 (0.005)c

n/a= no data collection.
** different superscript means significantly different at $p<0.05$ (t-test).

(b) Parent rosette petioles

Month	Site		
	Port Meadow submerged	Port Meadow non-submerged	Open University
February	0.294 (0.011)g	0.220 (0.007)d	0.244 (0.007)ef
March	0.188 (0.007)c	0.187 (0.003)c	0.242 (0.004)e
April	0.287 (0.007)g	0.260 (0.005)f	n/a
May	0.297 (0.014)g	0.197 (0.004)c	n/a
June	0.149 (0.006)b	0.094 (0.009)a	0.146 (0.015)b

(c) Parent rosette underground structures

Month	Site		
	Port Meadow submerged	Port Meadow non-submerged	Open University
February	0.674 (0.011)j	0.536 (0.014)g	0.314 (0.010)c
March	0.632 (0.012)i	0.575 (0.005)h	0.374 (0.007)d
April	0.414 (0.009)e	0.312 (0.006)c	n/a
May	0.285 (0.017)c	0.316 (0.008)c	n/a
June	0.147 (0.009)a	0.220 (0.009)b	0.489 (0.045)f

Table 4.4 continued

(d) Stolons

Month	Site		
	Port Meadow submerged	Port Meadow non-submerged	Open University
May	0.054 (0.002)[a]	0.107 (0.005)[b]	n/a
June	0.363 (0.011)[c]	0.434 (0.010)[d]	0.581 (0.032)[e]

(e) Ramet leaves

Month	Site		
	Port Meadow submerged	Port Meadow non-submerged	Open University
May	0[a]	0.027 (0.001)[b]	n/a
June	0.159 (0.017)[d]	0.105 (0.005)[c]	0.082 (0.005)[b]

(f) Ramet petioles

Month	Site		
	Port Meadow submerged	Port Meadow non-submerged	Open University
May	0[a]	0.018 (0.001)[b]	n/a
June	0.100 (0.013)[d]	0.082 (0.005)[d]	0.072 (0.003)[c]

(g) Ramet underground structures

Month	Site		
	Port Meadow submerged	Port Meadow non-submerged	Open University
June	0.030 (0.004)[a]	0.007 (0.004)[b]	0.073 (0.003)[c]

(h) Floral structures

Month	Site		
	Port Meadow submerged	Port Meadow non-submerged	Open University
May	0[a]	0.074 (0.005)[b]	n/a
June	0.120 (0.006)[c]	0.074 (0.004)[b]	0.096 (0.010)[bc]

allocation to parent rosette leaves but there are not clear increases in allocation to these peaks earlier in the season (Table 4.4b). In contrast with allocation to parent rosette leaves, allocation to parent rosette petioles was (with the exception of March) greater in Port Meadow submerged site plants compared with Port Meadow non-submerged site plants.

Allocation to stolons only occurred during two months of the study, May and June. The Port Meadow non-submerged site plants always showed greater allocation to stolons than the Port Meadow submerged site plants (Table 4.4d). The Open University site plants showed very high stolon allocations compared to the other two sites.

As with stolons, allocation to floral structures only occurred during May and June. Although flowering in the Port Meadow submerged site plants began later than in the other two sites the floral allocation in June was significantly greater (Table 4.4h). There was no change in allocation to floral structures in Port Meadow non-submerged site plants in May and June. Allocation to flowering in June in Open University site plants was in between the two Port Meadow site values.

As with floral structures, although allocation to ramet leaves started later in Port Meadow submerged site plants compared to the other two sites, the allocation level in June was significantly greater (Table 4.4e). Although allocation to ramet petioles started later in the Port Meadow submerged site plants there was no significant difference between the Port Meadow sites in June (Table 4.4f). With allocation to ramet underground structures the Open University site plants show a very large allocation compared with the other two sites (Table 4.4g). The Port Meadow non-submerged site plants show the least allocation to ramet

underground structures.

The petioles:leaves dry weight allocation ratios show that the Port Meadow submerged site plants had a greater emphasis on petiole allocation relative to leaves throughout the study and especially early in the year (Table 4.5). Plants from both the Port Meadow sites show a similar pattern of change in the ratio, with an increase in allocation to leaves relative to petioles until May and then an increase in allocation to petioles relative to leaves in June (Table 4.5).

From the available data the stolons:ramets dry weight allocation ratios for the Open University and Port Meadow non-submerged site plants are very similar (Table 4.6). However, the Port Meadow submerged site plants show a much greater emphasis on **ramet allocation** relative to stolon allocation (Table 4.6).

The floral structures:stolons dry weight allocation ratios also show the Port Meadow submerged site plants to be distinct from the other populations (Table 4.7). The Port Meadow submerged site plants show a much greater emphasis on floral allocation relative to stolons compared with plants from the other populations (Table 4.7).

The below ground:above ground dry weight allocation ratios for February to April show that the Port Meadow submerged site plants have greater emphasis on below ground allocation ('root') relative to above ground allocation ('shoot') compared to the other populations (Table 4.8). During February and March the Open University site plants show a much greater emphasis on above ground allocation relative to below ground allocation compared to the other plants (Table 4.8). During May and June the two Port Meadow populations change positions with the Port

Table 4.5

Petioles:leaves dry weight allocation ratios (mean, per plant) for *R. repens* plants collected from the three field sites February to June 1983 (n as Table 4.2).

Month	Site		
	Port Meadow submerged	Port Meadow non-submerged	Open University
February	9.188	0.898	0.548
March	1.044	0.782	0.630
April	0.957	0.607	n/a
May	0.786	0.619	n/a
June	2.014	0.862	1.227

n/a= no data collection.

Table 4.6

Stolon:ramet dry weight allocation ratios (mean, per plant) for *R. repens* plants collected from the three field sites February to June 1983 (n as Table 4.2).

Month	Site		
	Port Meadow submerged	Port Meadow non-submerged	Open University
May	-	2.378	n/a
June	1.256	2.214	2.559

n/a= no data collection.

Table 4.7

Floral structures:stolons dry weight allocation ratios (mean, per plant) for *R. repens* plants collected from the three field sites February to June 1983 (n as Table 4.2).

Month	Site		
	Port Meadow submerged	Port Meadow non-submerged	Open University
May	-	0.692	n/a
June	0.331	0.171	0.165

n/a= no data collection.

Table 4.8

Below ground: above ground dry weight allocation ratios (mean, per plant) for *R. repens* plants collected from the three field sites February to June 1983 (n as Table 4.2).

Month	Site		
	Port Meadow submerged	Port Meadow non-submerged	Open University
February	2.067	1.155	0.453
March	1.717	1.353	0.597
April	0.706	0.453	n/a
May	0.399	0.462	n/a
June	0.215	0.297	1.283

n/a= no data collection.

Meadow non-submerged site plants showing the greater emphasis on below ground allocation relative to above ground (Table 4.8). Plants from both Port Meadow sites show a trend of increased emphasis on above ground allocation relative to below ground throughout the study period (Table 4.8).

4.3 Discussion

During submergence (February to April- see Appendix 1) the plants in the Port Meadow submerged site showed many of the characteristics of the submerged plants in experiments 1 & 2 (Chapter 3). These are a relatively high allocation to petioles and underground structures (Table 4.4b & c), a delay in flowering and ramet production (Table 4.3e,f & h), and lower total dry weights (Table 4.2).

These field results show an increase in sexual reproductive allocation and a decrease in vegetative reproduction allocation following submergence (Table 4.4). Submergence also appears to result in an increase in allocation to ramets relative to allocation to stolons (Table 4.6) and an increase in floral allocation relative to allocation to stolons (Table 4.7).

The fall in total dry weight in June for the Port Meadow non-submerged site plants may be linked to drought which was apparent at that site (Table 4.2). The Port Meadow submerged site was not droughted but the Open University site did appear to be which may explain the low June total dry weights at this site (Table 4.2). From the available data the Open University site plants appear very different from the Port Meadow plants. However, in terms of relative allocation to parent rosette

leaves, petioles and underground structures they resemble the Port Meadow non-submerged site plants.

These results must be interpreted with caution because the populations may be genetically distinct (Turkington, 1979) and they are growing under different environmental conditions (see Appendix 1) even after submergence has been accounted for. Differences in allocation patterns of field populations have often been found to disappear when plants are grown under a common environment, i.e. the differences in allocation were due to environmental differences, (e.g. Hickman, 1975; Abrahamson and Hershey, 1977; Holler and Abrahamson, 1977; Pitelka, 1977; Raynal, 1979).

Clearly, because of these findings field results **alone** can not be used in a discussion of strategy. However, several authors have used such data as the basis for strategic analysis (e.g. Abrahamson and Gadgil, 1973; Abrahamson 1975a; 1975b; Gaines et al, 1974; Smith, 1972).

Returning to the questions asked in the introduction:

1. Do dry weight allocation patterns differ between submerged and non-submerged plants under field conditions?

The dry weight allocation patterns for the Port Meadow site plants are clearly different and it is probable (taking the results of Chapter 3 into consideration) that many of these differences are related to the submergence of one of the sites. However, other environmental factors and the possibility of genetic differences discussed above can not be ignored. This is investigated in Chapter 5.

2. Are the allocation patterns of plants from the two distant non-submerged sites more alike than those of the two Port Meadow sites?

This is a difficult question to answer because of the lack of Open University site data, but the relative dry weight allocation suggests that the Port meadow non-submerged site plants are more like the Open University site plants than the Port Meadow submerged site plants. This is possibly related to the lack of submergence in both these sites. This will be investigated futher in Chapter 5.

3. How do these differences in allocation pattern (if any) compare with those found under controlled conditions (Chapter 3)?

The Port Meadow submerged site plants show the greater dry weight allocation to petioles and underground structures found in the submerged plants in Chapter 3. They also show a delay in stolon and flower production. The Port Meadow submerged plants, however, show a greater final allocation to floral structures but a lower allocation to stolons. This will be studied further in Chapter 5.

4.4 Summary

1. The dry weight allocation patterns of R. repens plants were compared under submerged and non submerged conditions in the field.

2. The results suggest that submergence influences dry weight allocation in the field.

3. Common environment studies are required to validate the findings in terms of strategic analysis.

Chapter 5

Dry Weight Allocation and Submergence in Ranunculus repens.

3. Genetic differentiation between populations.

"..examples of highly localized differentiation of plant populations over a few metres are common.."

(Turkington, 1979)

5.1 Introduction

The theoretical basis for studies of dry weight allocation in plants has been discussed (Chapter 1). In Chapter 3 the tactical differences in dry weight allocation associated with submergence of plants from one particular R. repens population were investigated. In Chapter 4 the differences in dry weight allocation in submerged and non-submerged field populations of R. repens were followed but the nature of these differences, whether strategic or tactical, is unknown.

The correct interpretation of these field results depends on the separation of these effects (Stearns, 1976; Harper, 1977). This is often achieved by growing plants from different habitats in a common environment (e.g. Douglas, 1981; Reinartz, 1984b). These are often termed 'transplant gardens' (Chapin and Chapin, 1981).

This chapter is concerned with the variations in strategy and tactics of dry weight allocation shown by R. repens populations from different sites (see Appendix 1) grown in a 'transplant garden'. The three

populations correspond with the populations studied in Chapter 4.

In contrast to earlier studies (e.g. Turesson, 1922) seeds were not used in this transplant experiment because of the uncertainty concerning how representative the traits shown by such plants are of the native population (Heslop-Harrison, 1964; Lovett Doust, 1981b).

The transplant garden experiment was extended beyond the usual single common environment to include a submergence treatment which could be used to investigate tactical differences in allocation patterns. The experimental results can be used to look at differences in the allocation pattern on two levels:

1. The allocation patterns of each population within each of the two treatments, strategic differences.

2. The tactical differences in allocation between the two treatments based on each population.

This approach is similar to that of Douglas (1981) who grew Mimulus primuloides at a range of densities under otherwise common environments and Mooney and Billings (1961) who grew Oxyria digyna in different photoperiods and temperatures under otherwise common environments.

5.2 Experimental Results

Rosettes of R. repens were transplanted from the three study sites (see Appendix 1) and either subjected to a one month submergence period followed by about 5 months growing in air, or to growing in air for the

whole period (details in section 2.4 as experiment 3).

Within each site-treatment group there was a large range of genet dry weights at harvest (Table 5.1). There is an overall significant effect of site, and of submergence and also an interaction between these factors on total dry weight (Table 5.1). However, only plants from the Port Meadow non-submerged site show significantly less total dry weight at harvest with submergence (Table 5.1). The Port Meadow non-submerged site plants under the control treatment (non-submerged) have significantly greater dry weights than all other site-treatment pairs (Table 5.1).

Overall all organ dry weights show a significant submergence treatment effect (Table 5.2). The effect of site on organ dry weights is significant in all but stolons and floral structures. However, the pair-wise t-test analysis shows that only plants from the Port Meadow non-submerged site show significantly different stolon dry weights (Table 5.2). Many organ dry weights show significant submergence treatment-site interactions

In the submergence treatment most organ weights are lower than control treatment organ weights (Table 5.2). Port Meadow non-submerged site plants show significantly lower dry weights of all organs due to the submergence treatment. With the exception of parent rosette underground structures and stolons, organ dry weights in the Port Meadow submerged site plants are significantly less in the submergence treatment. However, in the Open University site plants only the dry weight of floral structures is significantly less due to submergence (Table 5.2). No organ weights are significantly greater in the submergence treatment compared to the controls.

Table 5.1

Total dry weights (g, range and mean per plant) for pot grown *R. repens* plants in experiment 3. Plants were collected from the three field sites during January 1983 and subjected to submergence or control treatments and harvested in August 1983 (n= 10).

Site	Treatment	Total dry weights (g) Range	Mean
Port Meadow submerged	Control	45.9-118.3	76.1b**
Port Meadow submerged	Submergence	42.6-109.8	70.3ab
Port Meadow non-submerged	Control	76.5-119.2	105.1c
Port Meadow non-submerged	Submergence	36.4-78.2	57.1a
Open University	Control	49.5-90.5	64.6ab
Open University	Submergence	33.8-88.1	61.8ab

Pooled S.E. = 6.3
Anova: Site $p<0.05$; Treatment $p<0.001$; Interaction $p<0.001$.
** different superscript means significantly different at $p<0.05$ using pooled S.E. in t-test (see Mead and Curnow, 1983).

Table 5.2

Dry weights of organs (g, mean per plant) for pot grown R. repens plants. Plants were collected from the three field sites during January 1983 and subjected to submergence or control treatments and then harvested in August 1983 (n= 10).

Site	Treatment	Organ dry weights (g)					
		Stolons	Ramet Petioles	Ramet Leaves	Ramet Underground	Parent Rosette Underground	Floral Structures
Port Meadow submerged	Control	23.8a**	13.0c	12.2b	23.5bc	3.4c	0.23bc
Port Meadow submerged	Submergence	22.7a	9.5ab	8.3a	26.3cd	3.5c	0.07a
Port Meadow non-submerged	Control	33.5b	16.8d	19.7c	32.7d	2.2b	0.33c
Port Meadow non-submerged	Submergence	22.0a	7.4a	9.0a	17.4ab	1.1a	0.11ab
Open University	Control	27.1ab	9.7ab	12.1b	12.4a	3.0c	0.33c
Open University	Submergence	23.6a	10.8bc	10.1ab	14.2a	3.0c	0.04a
	Pooled S.E. =	2.49	1.01	0.99	2.31	0.21	0.05
Anova:	Site	n.s	n.s.	p<0.001	p<0.001	p<0.001	n.s.
	Treatment	p<0.01	p<0.001	p<0.001	n.s.	p<0.05	p<0.001
	Interaction	n.s.	p<0.001	p<0.001	p<0.001	p<0.05	n.s.

** different superscipt means significantly different at p<0.05 using pooled S.E. in t-test (see Mead and Curnow, 1983).

As detailed in the Introduction, dry weight allocation results can be studied on two levels. Firstly within each treatment, comparing the different populations (strategic differences) and secondly, within each population comparing the two treatments (tactical differences).

The within treatment results for the control treatment (Table 5.3) show that plants from the three populations have very different dry weight allocation patterns. Plants from the Open University site have the greatest dry weight allocations to stolons, parent rosette underground structures, floral structures and ramet leaves but the lowest allocation to ramet underground structures and are intermediate for allocation to ramet leaves (Table 5.3). The Port Meadow non-submerged site plants in the control treatment, have the lowest dry weight allocations for all organs except ramet underground structures for which their allocation is the greatest (Table 5.3). The Port Meadow submerged site plants show an intermediate level of dry weight allocation for all organs except ramet petioles for which their allocation is the highest (Table 5.3).

The allocation patterns under the submergence treatment are different from the above descriptions (Table 5.3). However, Open University site plants show the greatest (or equal highest) dry weight allocation to stolons, ramet petioles, ramet leaves and parent rosette underground structures (Table 5.3). There is no pattern of lower organ allocation levels in either Port Meadow site in the submergence treatment (Table 5.3).

Overall, the Open University site plants show relatively low allocations to ramet underground structures and relatively high allocation to stolons, ramet leaves and parent rosette underground structures (Table 5.3).

Table 5.3

Dry weight allocations to organs (mean and S.E. per plant, based on graphical technique - see section 2.6) for pot grown *R. repens* plants. Plants were collected from the three field sites during January 1983 and subjected to submergence or control treatments and then harvested in August 1983 (n= 10).

Site	Treatment	Dry weights allocations to organs					
		Stolons	Ramet Petioles	Ramet Leaves	Ramet Underground	Parent Rosette Underground	Floral Structures
Port Meadow submerged	Control	0.261 (0.013)^{a**}	0.190 (0.008)^{a}	0.182 (0.007)^{a}	0.327 (0.011)^{a}	0.029 (0.001)^{a}	0.007 (0.0003)^{a}
Port Meadow submerged	Submergence	0.365 (0.006)^{b}	0.102 (0.004)^{b}	0.082 (0.003)^{b}	0.421 (0.004)^{b}	0.026 (0.002)^{a}	0.004 (0.001)^{b}
Port Meadow non-submerged	Control	0.260 (0.019)^{a}	0.067 (0.004)^{c}	0.083 (0.004)^{b}	0.561 (0.021)^{c}	0.027 (0.001)^{a}	0.002 (0.0003)^{c}
Port Meadow non-submerged	Submergence	0.488 (0.014)^{c}	0.148 (0.003)^{d}	0.039 (0.003)^{c}	0.295 (0.016)^{a}	0.021 (0.001)^{b}	0.008 (0.001)^{a}
Open University	Control	0.452 (0.020)^{c}	0.165 (0.011)^{ad}	0.210 (0.013)^{d}	0.120 (0.007)^{d}	0.041 (0.002)^{c}	0.014 (0.001)^{d}
Open University	Submergence	0.500 (0.014)^{c}	0.151 (0.013)^{d}	0.186 (0.009)^{a}	0.116 (0.007)^{d}	0.045 (0.002)^{c}	0.002 (0.001)^{c}

** different supersript means significantly different at $p<0.05$ (t-test).

The different dry weight allocation patterns in the two treatments show that tactical differences in allocation do exist (Tables 5.3 & 5.4). However, in the Open University site only floral allocation shows a significant difference. Port Meadow non-submerged site plants show significantly greater allocation to stolons, ramet petioles and floral structures but less allocation to ramet leaves, ramet underground structures and parent ramet underground structures (Tables 5.3 & 5.4). Port Meadow submerged site plants show significantly greater dry weight allocation to stolons and ramet underground structures and less allocation to floral structures, ramet leaves and ramet petioles but no difference in allocation to parent rosette underground structures (Tables 5.3 & 5.4).

The overall pattern of tactical differences shows that only allocation to stolons is either greater or the same in the submergence treatment, whereas both ramet leaves and parent rosette underground structures show either less or the same allocation (Table 5.4). Allocation to floral structures, ramet underground structures, and ramet petioles show variable differences due to submergence depending on the site of origin of the plants.

The ramet petioles:ramet leaves dry weight allocation ratios (Table 5.5) show that plants from both the Port Meadow sites have greater emphasis on petioles, relative to leaves, with submergence. This increase is particularly large for the Port Meadow non-submerged site plants (Table 5.5). Plants from the Open University site show no differences in this ratio.

Plants from both Port Meadow sites show opposite differences in the below ground:above ground dry weight allocation ratios (equivalent to

Table 5.4

Tactical differences in dry weight allocation to organs in pot-grown *R. repens* plants in experiment 3 resulting from the submergence treatment (see Table 5.3).

Organ	Site		
	Port Meadow submerged	Port Meadow non-submerged	Open University
Stolons	greater**	greater	no difference
Ramet Petioles	lesser	greater	no difference
Ramet Leaves	lesser	lesser	no difference
Ramet Underground	greater	lesser	no difference
Parent Rosette Underground	no difference	lesser	no difference
Floral Structures	lesser	greater	lesser

** differences are significant at $p<0.05$ (t-test).

Table 5.5

The ramet petioles:ramet leaves dry weight allocation ratios (see Table 5.3) for pot-grown *R. repens* plants in experiment 3. Plants were collected from the three field sites during January 1983 and subjected to submergence or control treatments and harvested in August 1983 (n= 10).

Treatment	Site		
	Port Meadow submerged	Port Meadow non-submerged	Open University
Control	1.04	0.81	0.79
Submergence	1.24	3.79	0.81

Table 5.6

The below ground:above ground dry weight allocation ratios (see Table 5.3) for pot-grown *R. repens* plants in experiment 3. Plants were collected from the three field sites during January 1983 and subjected to submergence or control treatments and harvested in August 1983 (n= 10).

Treatment	Site		
	Port Meadow submerged	Port eadow non-submerged	Open University
Control	0.553	1.426	0.191
Submergence	0.808	0.468	0.192

'root:shoot' ratios) with submergence (Table 5.6). The Port Meadow submerged site plants show greater allocation to below ground structures relative to above ground structures with the submergence treatment (Table 5.6). The Open University site plants show no difference in this ratio but overall have a relatively high emphasis on above ground allocation relative to below ground allocation compared to the other populations (Table 5.6).

The stolons:ramets dry weight allocation ratios show that again the Open University site plants are distinct from the other two populations (Table 5.7). Plants from both the Port Meadow sites show greater allocation to stolons relative to ramets with the submergence treatment, with the Port Meadow non-submerged site plants showing the greater difference. In the control treatment the Open University site plants show a relatively high allocation to stolons compared to ramets (Table 5.7).

Plants from both the Open University and Port Meadow submerged sites have lower floral structures:stolons dry weight allocation ratio in the submergence treatment. This reveals decreased allocation to floral structures relative to stolons with submergence (Table 5.8). The Port Meadow non-submerged site plants have the opposite change with an increased emphasis on floral allocation relative to stolon allocation (Table 5.8).

Table 5.7

The stolons:ramets dry weight allocation ratios (see Table 5.3) for the pot-grown *R. repens* plants in experiment 3. Plants were collected from the three field sites during January 1983 and subjected to submergence or control treatments and harvested in August 1983 (n= 10).

Treatment	Site		
	Port Meadow submerged	Port Meadow non-submerged	Open University
Control	0.379	0.366	0.913
Submergence	0.603	1.010	1.104

Table 5.8

The floral structures:stolons ($x10^{-2}$) dry weight allocation ratios (see Table 5.3) for the pot-grown *R. repens* plants in experiment 3. Plants were collected from the three field sites during January 1983 and subjected to submergence or control treatments and harvested in August 1983 (n= 10).

Treatment	Site		
	Port Meadow submerged	Port Meadow non-submerged	Open University
Control	2.64	0.78	3.10
Submergence	1.10	1.64	0.40

5.3 Discussion

5.3.1 Genetic Differentiation Between Populations

Plants from the three populations show different dry weight allocation patterns in both transplant environments (submerged and non-submerged) and also different tactical differences in allocation associated with submergence (Table 5.4). These results show that the three populations are genetically distinct with respect to dry weight allocation strategies. This implies that the field dry weight allocation results can not be used to compare tactical allocation differences in submerged and non-submerged conditions.

The research of Turesson (1922) and Clausen et al, (1940; 1948) showed that genetic differentiation occurs within a species. Further research has since shown this to be a widespread phenomenon (e.g. Antonovics, 1972; Rochow, 1970; Chapin and Chapin, 1981; McNaughton, 1966; Douglas 1981). Many of these studies involved populations that were far apart, for example, over a range of altitudes. However, the results of this experiment show that genetic differentiation between R. repens populations can occur on a small scale, as well as on a large scale.

Plants in the two Port Meadow populations are only between 5 and 25 metres apart. Other reports of small scale genetic differentiation within a species are in the literature (e.g Aston and Bradshaw, 1966; Antonovics, 1972; Wu and Antonovics, 1975; Lovett-Doust, 1981a; 1981b Turkington, 1979; McGraw and Antonovics, 1983). Turkington and Harper (1979) showed that Trifolium repens clones were locally specialised within a single field and this was dependent on neighbouring species.

It was Turesson (1922) who coined the word 'ecotype' to describe genetic differentiation within a single species. However, implicit in this term was that the genetic variation increased the 'fitness' (by some measure) of the plant (Chapin, and Chapin, 1981; Lovett-Doust, 1981b). Claimed demonstrations of this have been reported for a variety of species (e.g. Turesson, 1922; Clausen et al, 1940; McMillan, 1959; Bradshaw et al, 1964; McNaughton, 1966; Callaghan, 1974; Turkington and Harper, 1979; Chapin and Chapin, 1981). However, Quinn (1978) points out that the term has come, by usage, to mean any degree of genetic differentiation within a species without any qualification.

Although ecotypes have been associated with the frequency of submergence (Keeley, 1979) and drought (Ashenden et al., 1975), more research is required to establish the existence of a submergence (or drought?) ecotype (in the strict sense of Turesson (1922)) of R. repens at the Port Meadow submerged site.

5.3.2 Tactical Allocation Differences

5.3.2.1 The Maintenance of Stolon Allocation

Stolons are the only organ in which allocation is the same (Open University site plants) or greater (Port Meadow sites) in the submergence treatment (Tables 5.3 & 5.4). This supports the findings in experiment 2 (Chapter 3) that stolon allocation is maintained in Open University site plants in response to submergence.

Ginzo and Lovell (1973a) found that (percentage) allocation to stolons in R. repens did not change in response to nitrogen stress. Increased

(percentage) allocation to vegetative reproduction has often been associated with decreased nutrient levels in rhizomatous clonal perennials (Andel and Vera, 1977; Ogden, 1974). However, vegetative reproduction is not always increased in stress conditions. Increased density has been shown to result in decreased vegetative reproductive allocation in rhizomatous and stoloniferous clonal perennials (Andel and Vera, 1977; Ogden, 1974; Holler and Abrahamson, 1977). Also Williams (1970) predicts decreased allocation to vegetative reproduction under density stress from a model of a clonal perennial.

Perhaps dry weight allocation to stolons is unchanged, or greater, because of the importance of stolons (with their ramets) in the maintenance of population growth in R. repens (Sarukhan and Gadgil, 1974; Soane and Watkinson, 1979). This emphasis on vegetative allocation may be associated with the 'getting away' strategy proposed by Ginzo and Lovell (1973a; 1973b) for R. repens. The nitrogen deficient plants had fewer, longer stolons. They suggest that this increases the probability that ramets were placed further away from the parent in unfavourable conditions. A similar strategy has been suggested by Hartnett and Bazzaz (1983) for Solidago canadensis. They found that ramets on severed rhizomes produced fewer longer rhizomes and they suggest that this is related to nutrient depletion.

This emphasis on stolon allocation can also be seen in the stolon:ramet dry weight allocation ratio, which can be considered as a crude measure of investment in spread (via stolons) against investment in vegetative offspring. The latter point is emphasized by the finding that ramet mortality is often size-related, the larger the ramet the lower the mortality risk (Pitelka et al, 1985). Although plants from the three populations have different detailed allocation patterns in response to

submergence they all show increased investment into stolons relative to ramets with submergence (Table 5.7).

5.3.2.2 Differences in Floral Allocation

The Port Meadow non-submerged site plants stand apart from the other plants with respect to the greater floral allocation with submergence (Table 5.3). However, the low number of flowering plants in the submergence treatment meant that the slope allocation results for these plants were difficult to determine; therefore, these results should be interpreted with caution.

This emphasis on floral allocation is also apparent in the floral structures:stolon dry weight allocation ratios (Table 5.8). This ratio can be considered as a measure of the relative emphasis on vegetative reproductive allocation against sexual reproductive allocation. This measure takes no account of the initial vegetative investment made by the plants into ramets but to include any ramet dry weight would introduce a much greater error due to the dry weight gained independently by the ramets. For this reason most authors leave out ramet allocation from considerations of vegetative reproduction (e.g. Smith, 1972; Pitelka et al, 1985).

In general both nutrient and density stresses have been shown to result in maintained or reduced allocation (as percentages) to sexual reproduction (Harper and Ogden, 1970; Ogden, 1974; Thomas and Dale, 1974; Abrahamson, 1975a; Kawano and Nagai, 1975; Raynal and Bazzaz, 1975; Snell and Burch, 1975; Pemadasa, 1976; Abrahamson and Hershey, 1977; Andel and Vera, 1977; Holler and Abrahamson, 1977; Amarasinghe and

Pemadasa, 1982; Waite and Hutchings, 1982; Steen, 1984). A few researchers have found increased sexual reproductive allocation with stress. Polygonum cascadense increases allocation with 'harsher' conditions (Hickman, 1975) and Helianthus annuus with decreased light intensity (Hiroi and Monsi, 1966). However, these are both annual plants and no research has shown an increase in reproductive allocation in a perennial plant with increased stress. The increase in floral allocation in the Open University plants needs further investigation before it can seriously be considered.

5.3.2.3 Tactical Allocation Differences in Vegetative Organs

Differences in the ramet petioles:ramet leaves allocation ratio with submergence show that, despite opposite tactical differences in ramet petiole allocation (Table 5.4), the Port Meadow site plants increase their emphasis on ramet petioles relative to ramet leaves (Table 5.5). An emphasis on allocation to petioles was found in the recently submerged plants in Chapter 3 and this was related to the role of petioles in getting leaves to the surface of the water. However, the ramets in this experiment have never been submerged since they developed after submergence and so the same reasoning can not be used. Perhaps it is related to the possibility of submergence if submergence of the parent rosette has already occurred?

The emphasis on underground structures relative to above ground, found in the recently submerged plants in Chapter 3 was only found in the Port Meadow non-submerged site plants (Table 5.6). The lack of this emphasis in the Port Meadow submerged site plants may be another part of the suggested 'getting away' strategy, with an emphasis on above ground

structures leading to getting the plant away from an unfavourable site and not 'riding out' stresses using stored underground reserves.

5.3.3 Strategic Differences in Allocation

Genetically-based increased emphasis on vegetative reproduction is often associated with the stresses imposed by increased altitude and latitude (e.g. Mooney and Billings, 1961; McNaughton, 1966; Harris, 1970). This is however, not always the case. Douglas (1981) found that with increased altitude Mimulus primuloides plants showed a decreased emphasis on asexual reproduction which was genetically controlled. There is also some evidence of genetically-based decreased emphasis on sexual reproduction with these 'stresses', i.e. fewer flowers (Rochow, 1970; Mooney and Billings, 1961) and fewer seeds (Johnson and Cook, 1968).

The results here show that the Open University site plants have greater allocation to stolons and this may be related to the frequency of drought and/or mowing. Genetic differentiation has been shown to occur with drought and different cutting regime in Dactylis glomerata (Norris and Thomas, 1982; Ashenden et al, 1975). Also, McNeilly (1981) has shown drought-related genetic differentiation in Poa annua. Harper (1957) points out that R. repens is not very drought tolerant and is usually excluded from droughted habitats in the presence of competition from other plants. This may explain the importance of drought in the Open University site.

5.3.4 Problems with 'Transplant Gardens'

One of the main problems with the transplant garden results is that the plants can be completely different from those in the field (for example, mean total dry weights of less than 1g in the field compared with 57-105g in the transplant garden). This is often due to lack of competition in the transplant site. Douglas (1981) partially overcame this problem by growing plants under common environments but a range of densities. Lovett Doust (1981b) takes this approach to its logical conclusion by transplanting from site to site so as to take in all environment variables in two common environments. Some researchers have established transplant gardens at the site of each population so as to account for environment and edaphic variables but remove biotic factors (e.g. Harris, 1970; Chapin and Chapin, 1981).

Another criticism of transplant gardens is that if plant material (other than seed) is used, carry-over effects from the different environments may affect the results. However, McGraw and Antonovics (1983) suggest that growing the collected plants for one month prior to experimentation is sufficient to remove, or at least reduce the importance, of this factor.

5.4 Summary

1. Differences in dry weight allocation under transplant garden conditions led to the conclusion that the three populations are genetically distinct.

2. This is another example of localised genetic differentiation within a

single species.

3. As in the short term experiments (Chapter 3) dry weight allocation to stolons is maintained (or increased) following submergence

Chapter 6

Flowering and Submergence in Ranunculus repens

"Carrots do not ponder differential reproductive success"

(Ghiselin, 1974:41)

6.1 Introduction

It is clear from the previous chapters that seasonal submergence has large effects on subsequent growth in R. repens and this includes flowering and reproductive allocation. However, unlike many plants flowering and seed production (i.e. sexual reproduction) in R. repens represents only one of the possible means of colonisation and spread, the other being the production of ramets borne on stolons (i.e. vegetative reproduction).

Demographic studies on this species have shown that recruitment from seed is of minor importance in established populations (Sarukhan, 1971; 1974; Sarukhan and Harper, 1973; Lovett Doust, 1981a). Sarukhan and Gadgil (1974) modelled the population growth of R. repens and found that it was very sensitive to changes in ramet production but changes in the establishment of seedlings have very little effect on population growth. However, Soane and Watkinson (1979) found that seedling recruited plants made a significant contribution to the overall genetic diversity of the population. Establishment from seedlings will be essential in the colonisation of areas away from existing populations.

Given this background one could predict a continuum of possible strategies for changes in sexual and asexual reproduction in response to seasonal submergence. From the total cessation of flowering and seed production and concentration on ramet production to an increase in flowering and seed production with increases possibility of colonising new perhaps more favourable areas away from the submerged area, with no ramet production.

This chapter investigates the strategy or strategies shown by R. repens plants from the three study sites.

6.2 Field Observations and Measurements

Field observations on the Port Meadow sites (see Appendix 1) during 1982 had suggested a delay in flowering on the submerged site compared to the non-submerged site. This was investigated in more detail in 1983, on the same sites and the Open University site (see Appendix 1).

The submerged site plants showed a delay in flowering (Table 6.1) compared with the plants in both non-submerged sites. However, the number of flowers per plant was recorded only until June (Table 6.2) (see section 2.4 for field methods). There was no significant difference between the two Port Meadow populations but the Open University site plants had significantly fewer flowers compared with Port Meadow submerged site plants.

At Port Meadow submerged site plants were submerged until late May (May 1983 was an exceptionally wet month) and this may have prevented flower development during May, for example, by changes in the light climate

Table 6.1

The timing of flower production in the three field populations of *R. repens* (1983).

Site	Month					
	February	March	April	May	June	July
Port Meadow submerged	No**	No	No	No	Yes	Yes
Port Meadow non-submerged	No	No	No	Yes	Yes	Yes
Open University	No	No	No	Yes	Yes	Yes

** No = no plant flowering; Yes = some plants flowering.

Table 6.2

The number of flowers (per plant, mean and S.E.) for *R. repens* plants in the three field sites in June 1983 (n= 10).

Site	Flowers/plant
Port Meadow submerged	3.2 (0.5)^{a}**
Port Meadow non-submerged	2.2 (0.2)^{ab}
Open University	1.6 (0.4)^{b}

** as in all tables different superscripts mean significantly different at $p<0.05$ (t-test).

affecting photoperiodic and photomorphogenic responses. The differences in the number of flowers per plant could be due to other site differences, such as drought, and so controlled conditions are required before these differences can be interpreted as submergence-related.

6.3 Experimental evidence

Further evidence for a delay in flowering comes from experiment 2 (see section 2.4 and Chapter 3) where rosettes from the Open University site were submerged for varying lengths of time during Spring 1982. The plants were allowed to flower until the middle of June. None of the submerged plants flowered before the end of the experiment but half of the control (non-submerged) plants had flowers (Table 6.3).

These results are for plants from the Open University site and as genetic differentiation has been shown to exist between the different site populations further evidence is required. This delay may or may not have resulted in a reduction in flowering.

Experiment 3 (section 2.4 for methods) involved the submergence of plants collected from all three sites under controlled conditions. Some plants from each site were submerged for 4 weeks during February 1983 while others were left as controls.

The results for flowering are quite complex because a delay in flowering is confused by a reduction in the number of plants flowering (Table 6.4a). If the results are expressed as a percentage of the plants which finally flowered then there is some delay in the plants from the Open University and Port Meadow non-submerged site (Table 6.4b). Clearly,

Table 6.3

The number of *R. repens* plants flowering in experiment 2 by treatment.

Treatment	n	Number of flowering plants
Controls	11	6
4-week submerged	12	0
8-week submerged	6	0

Table 6.4a

The number of *R. repens* plants flowering with time in experiment 3. Plants were collected from the three field sites during January 1983 and subjected to a submergence or control treatment (n= 10).

Site	Treatment	Date (1983) 13/5	27/5	15/6	28/6
Port Meadow submerged	Control	0	3	6	6
Port Meadow submerged	Submergence	0	1	2	2
Port Meadow non-submerged	Control	0	5	10	10
Port Meadow non-submerged	Submergence	0	3	3	5
Open University	Control	0	1	8	9
Open University	Submergence	0	0	1	2

the greatest effect is on the number of plants flowering rather than a delay in flowering.

Comparing the number of plants flowering in the control treatments from each site, only six out the possible ten Port Meadow submerged site plants flowered whereas in the other two sites nine and ten plants flowered out of the possible ten (Table 6.4a). This suggests that Port Meadow submerged site plants are less likely to flower under non-submerged conditions. However, when the reduction in the number of flowering plants due to the submergence treatment is studied (4 for the Port Meadow submerged site, 5 for the Port Meadow non-submerged site and 7 for the Open University site) then the other two sites show the greater loss. Chi-squared tests (see section 2.5) on the effect of submergence on the number of plants flowering within each 'site' showed that the reduction was significant in the Open University and Port Meadow non-submerged site plants (at $p<0.05$) but not in the Port Meadow submerged site plants (Chi-squared= 3.33; d.f.= 1).

The average number of flowers per plant (Table 6.5) shows a substantial and significant reduction due to submergence in all three sites. However, if the zeros for the non-flowering plants are removed from the analysis (i.e. considering flowering plants only) (Table 6.6) only plants from the Port Meadow non-submerged and Open University sites still show a significant reduction in the number of flowers per plant in the submergence treatment.

Table 6.4b

The number of *R. repens* plants flowering with time as a percentage of the total number of flowering plants within each treatment in experiment 3. Plants were collected from the three field sites during January 1983 and subjected to a submergence or control treatment (n as 28/6 column in Table 6.4a).

Site	Treatment	Date (1983) 13/5	27/5	15/6	28/6
Port Meadow submerged	Control	0	50	100	100
Port Meadow submerged	Submergence	0	50	100	100
Port Meadow non-submerged	Control	0	50	100	100
Port Meadow non-submerged	Submergence	0	60	60	100
Open University	Control	0	11	89	100
Open University	Submergence	0	0	50	100

Table 6.5

The number of flowers (mean per plant) for *R. repens* plants collected from the three field sites in January 1983 and subjected to either a submergence or control treatment and harvested in August 1983 (experiment 3; n= 10).

Treatment	Site: Port Meadow submerged	Port Meadow non-submerged	Open University
Control	3.2^{bc}**	4.3^{c}	4.5^{c}
Submergence	0.9^{ba}	1.5^{ba}	0.5^{a}

Pooled S.E. = 0.60
Anova: Site n.s.;Treatment $p<0.001$;Interaction n.s.
** different superscript means significantly different at $p<0.05$ using pooled S.E. in t-test (see Mead and Curnow, 1983).

Table 6.6

The number of flowers (mean and S.E. per plant) for flowering *R. repens* plants alone. Plants were collected from the three field sites in January 1983 and subjected to either a submergence or control treatment and harvested in August 1983 (experiment 3, n as 28/6 column in Table 6.4a).

Treatment	Site		
	Port Meadow submerged	Port Meadow non-submerged	Open University
Control	5.3 (0.7)^{a**}	4.3 (0.1)^{a}	5.0 (0.9)^{ac}
Submergence	4.5 (2.5)^{ab}	3.0 (0.3)^{bc}	2.5 (0.5)^{b}

** different superscript means significantly different at $p<0.05$ (t-test).

6.4 The Control of flowering

6.4.1 Total plant dry weight

In Chapter 2 (section 6) it was shown that the dry weights of various organs are positively correlated with total dry weight. This was also the case for the dry weights of floral structures. This raises the possibility of the existence of a minimum dry weight before flowering will occur. This idea was tested using the data collected in experiment 3 for total dry weights and flowering behaviour.

The mean total dry weight of all the non-submerged plants (controls) that flowered was significantly greater than for those non-submerged plants that did not flower (Table 6.7). This reflects the trend that the probability of flowering increases with increasing total dry weight (Figure 6.1). All plants above a total dry weight of 70g flowered but several plants below this level also flowered (the lightest being 49.5g). This implies that if dry weight does control flowering then it is a crude control rather than a precise one. The reason for this apparent crude 'control' may be because the 'decision' to flower was made before the end of June and based on total dry weight at that time, whereas the total dry weights are for the harvest in mid-August.

The results for the submerged plants are similar, with a significant difference between the mean total dry weight for flowering and non-flowering plants (Table 6.8) but the mean total dry weight of flowering plants is significantly lower than that for the control treatment flowering plants (Tables 6.7 & 6.8). The relationship between the probability of flowering and total dry weight in the submergence treatment plants is also more complex (Figure 6.2).

Table 6.7

Total dry weight (mean and S.E.) of flowering and non-flowering *R. repens* plants (independent of site) in the control (non-submerged) treatment of experiment 3. The plants were collected from the field sites in January 1983 and harvested in August 1983.

	Total dry weight (g/plant)	n
Flowering	87.7 (4.8)a	25
Non-flowering	52.8 (3.0)b	5

Table 6.8

Total dry weight (mean and S.E.) of flowering and non-flowering *R. repens* plants (independent of site) in the submergence treatment of experiment 3. The plants were collected from the field sites in January 1983 and harvested in August 1983.

	Total dry weight (g/plant)	n
Flowering	77.7 (6.4)a	9
Non-flowering	56.8 (3.8)b	21

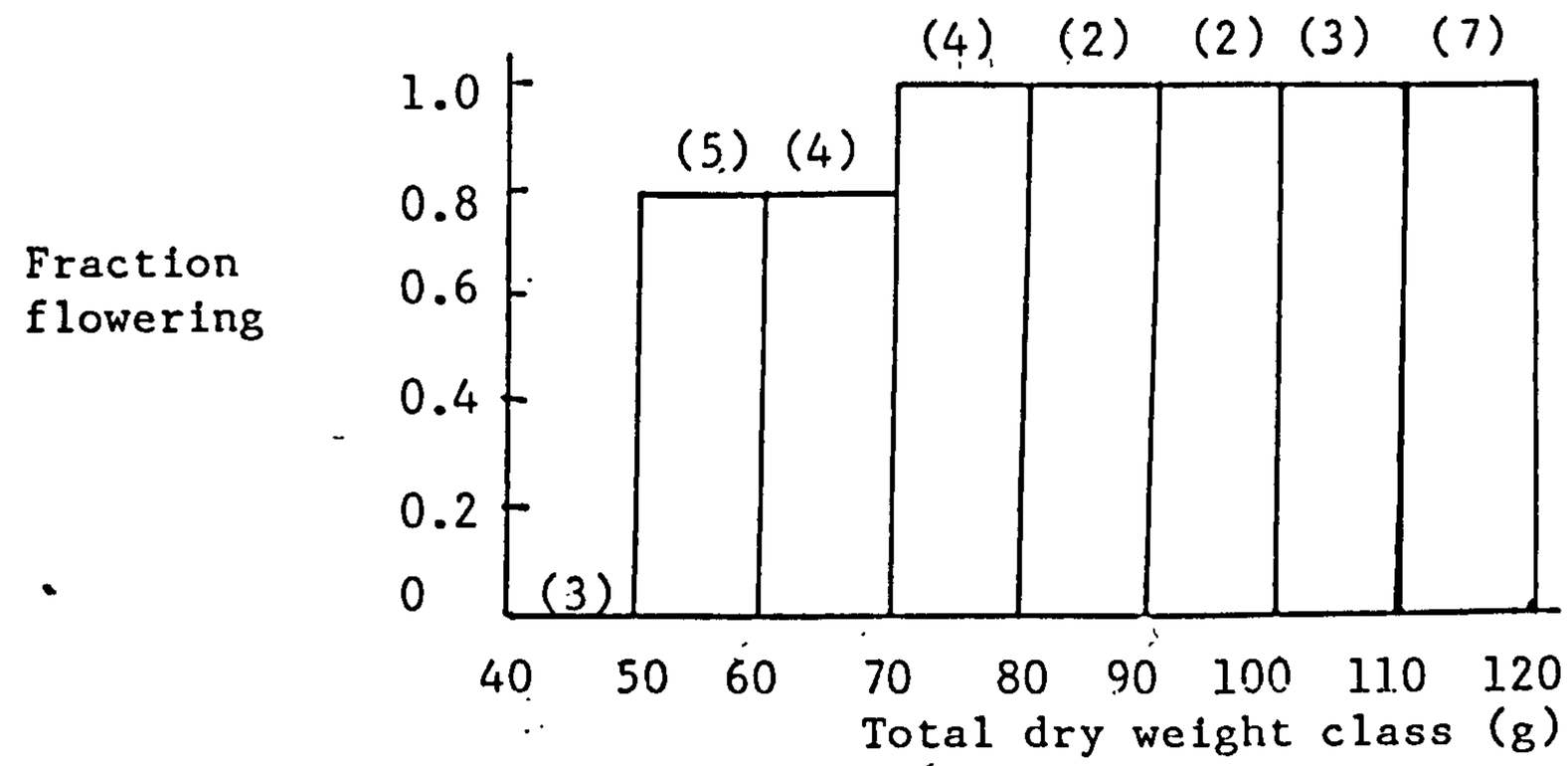


Figure 6.1

Fraction of R. repens plants flowering in each total dry weight class (n in brackets) for the control plants in experiment 3.

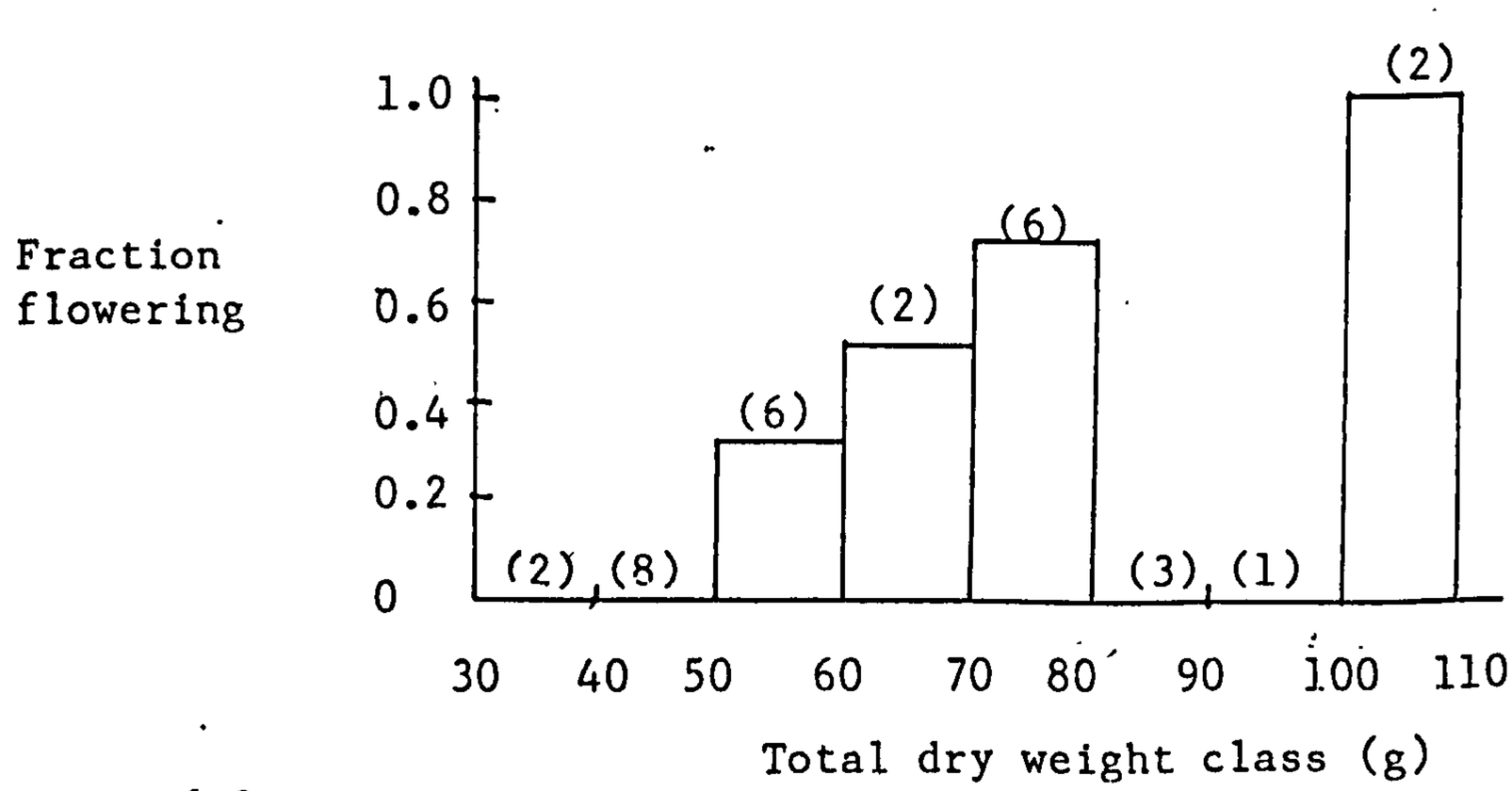


Figure 6.2

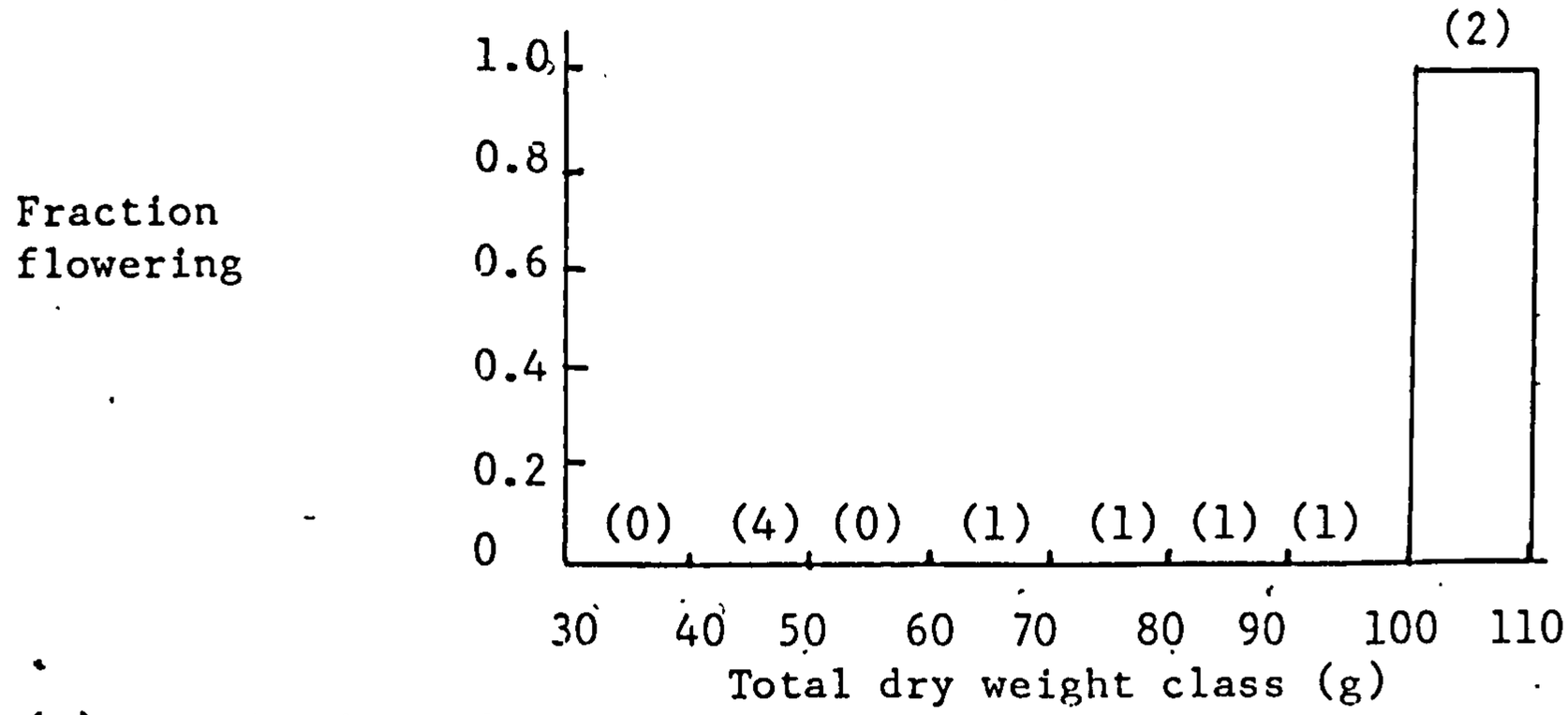
Fraction of R. repens plants flowering in each dry weight class (n in brackets) for the submergence treatment plants in experiment 3.

However, if the probability of flowering is plotted against total dry weight for each site group within the submerged treatment the pattern becomes much clearer (Figure 6.3). The Port Meadow non-submerged site plants show a similar pattern to the control plants except that all plants above 60g, not 70g, flowered. In the Port Meadow submerged site plants the cut-off is much higher with only plants with total dry weights above 100g flowering. The Open University site plants do not conform to any obvious pattern. Clearly the relationship between total dry weight and flowering has been altered for the plants from all three sites and in different ways.

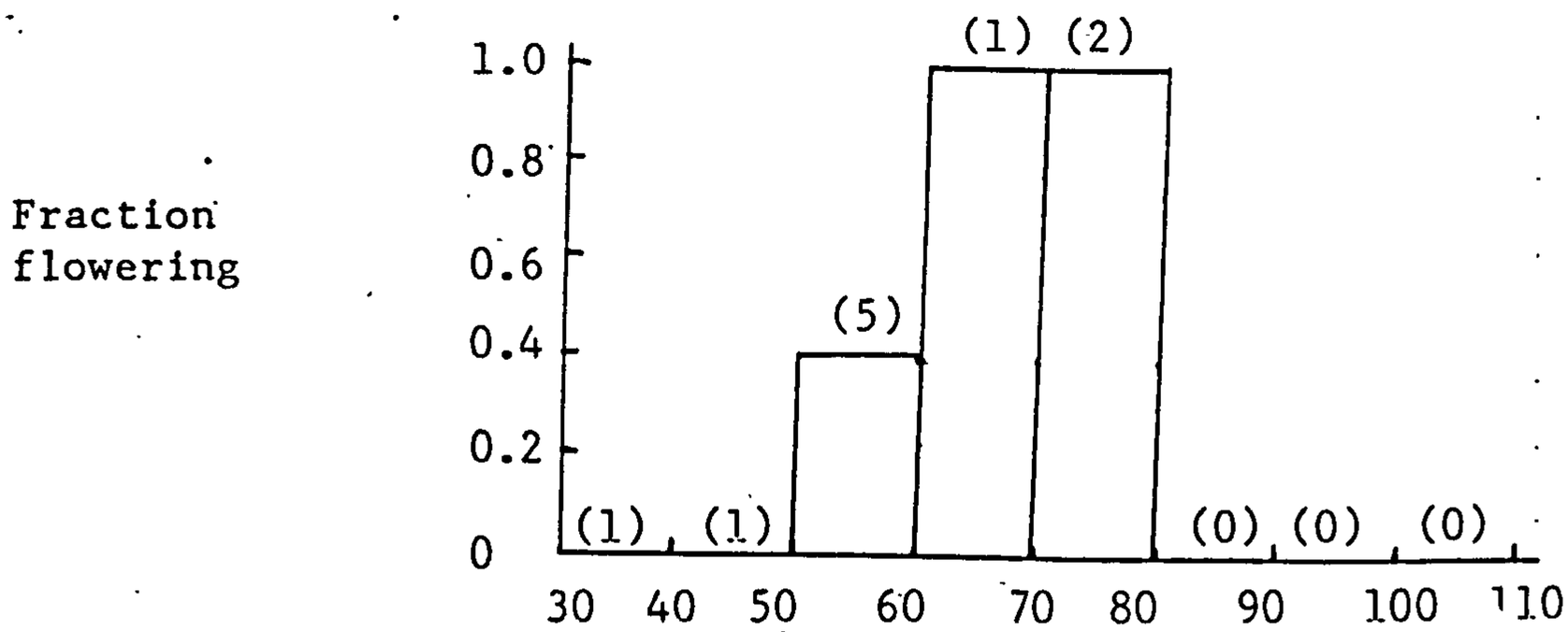
There is some field evidence of a positive correlation between flowering and total dry weight. Flowering and non-flowering genets were collected from the Port Meadow non-submerged site during May 1983 (section 2.4) and all the flowering genets had a total dry weight of above 0.8g (Figure 6.4); this is much less than the 70g 'threshold' found in experiment 3!

6.4.2 Ramet Density

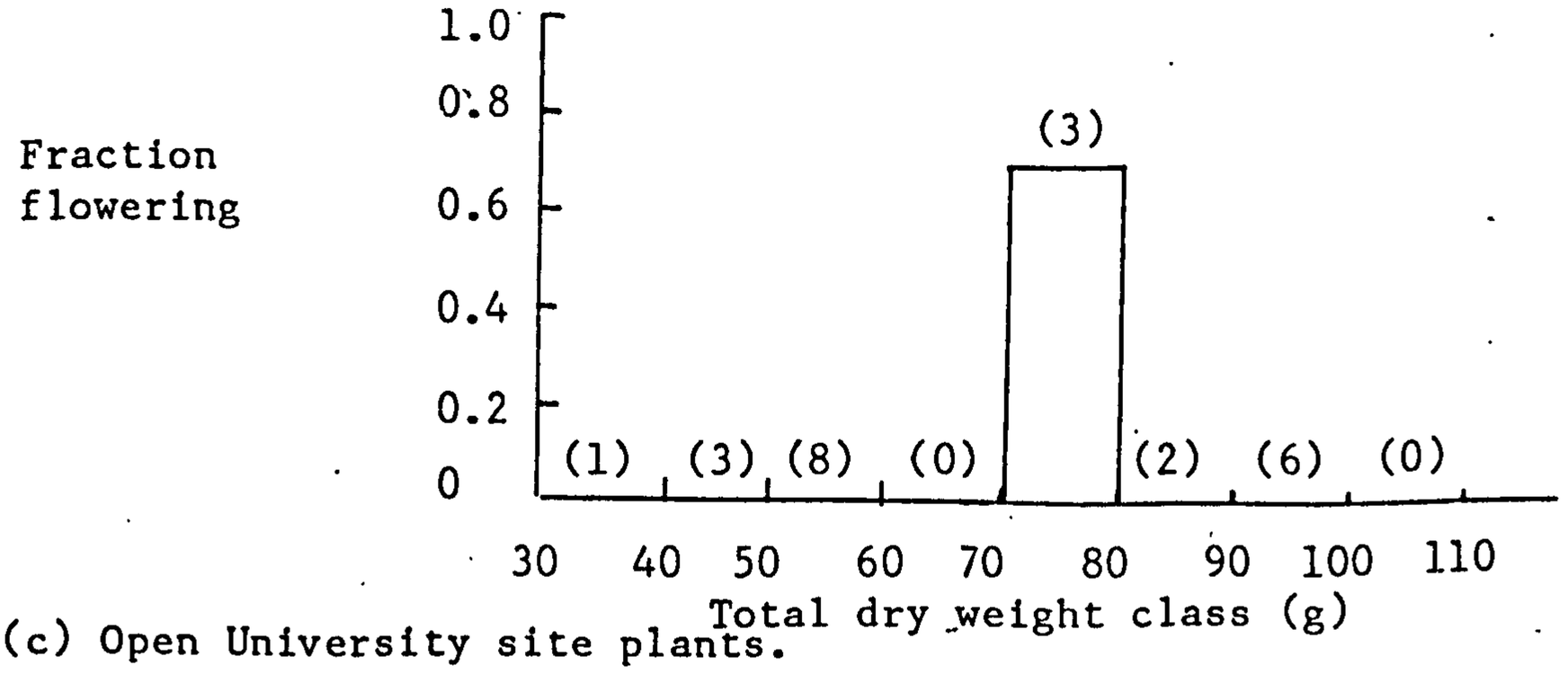
Total dry weight is a fairly good predictor of flowering behaviour and the relationship is modified by submergence. However, it was noted that the Port Meadow submerged site plants that did not flower under the submergence treatment (experiment 3), even though their total dry weights were well over 70g had very low ramet densities (number of ramets/pot). When ramet density and the probability of flowering are plotted for all plants in the submergence treatment, a definite pattern appears (Figure 6.5). The same is true for the non-submerged (control) plants (Figure 6.6) and the relationship is different.



(a) Port Meadow submerged site plants.



(b) Port Meadow non-submerged site plants.



(c) Open University site plants.

Figure 6.3

Fraction of R. repens plants flowering in each dry weight class (n in brackets) for the submergence treatment in experiment 3, by site of origin of plants.

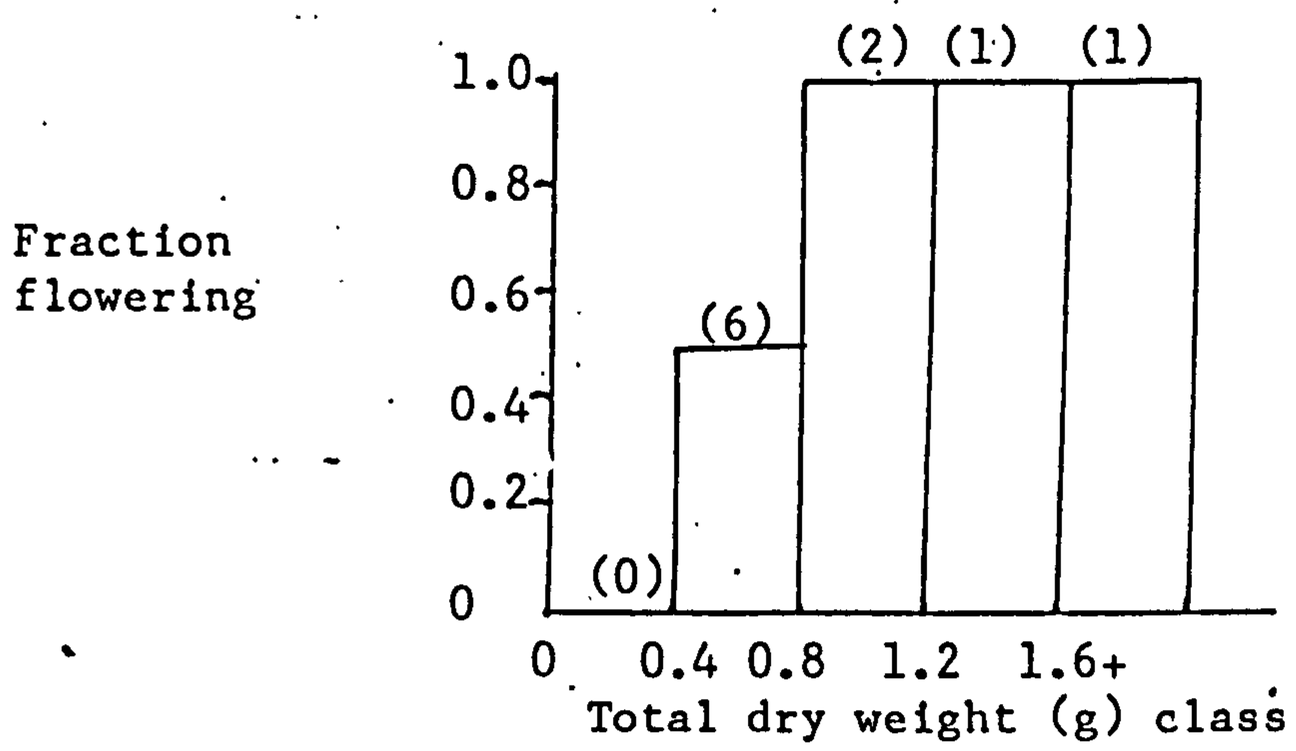


Figure 6.4

Fraction of plants flowering in each total dry weight class for R. repens collected from the Port Meadow non-submerged site in May 1983 (n = 10).

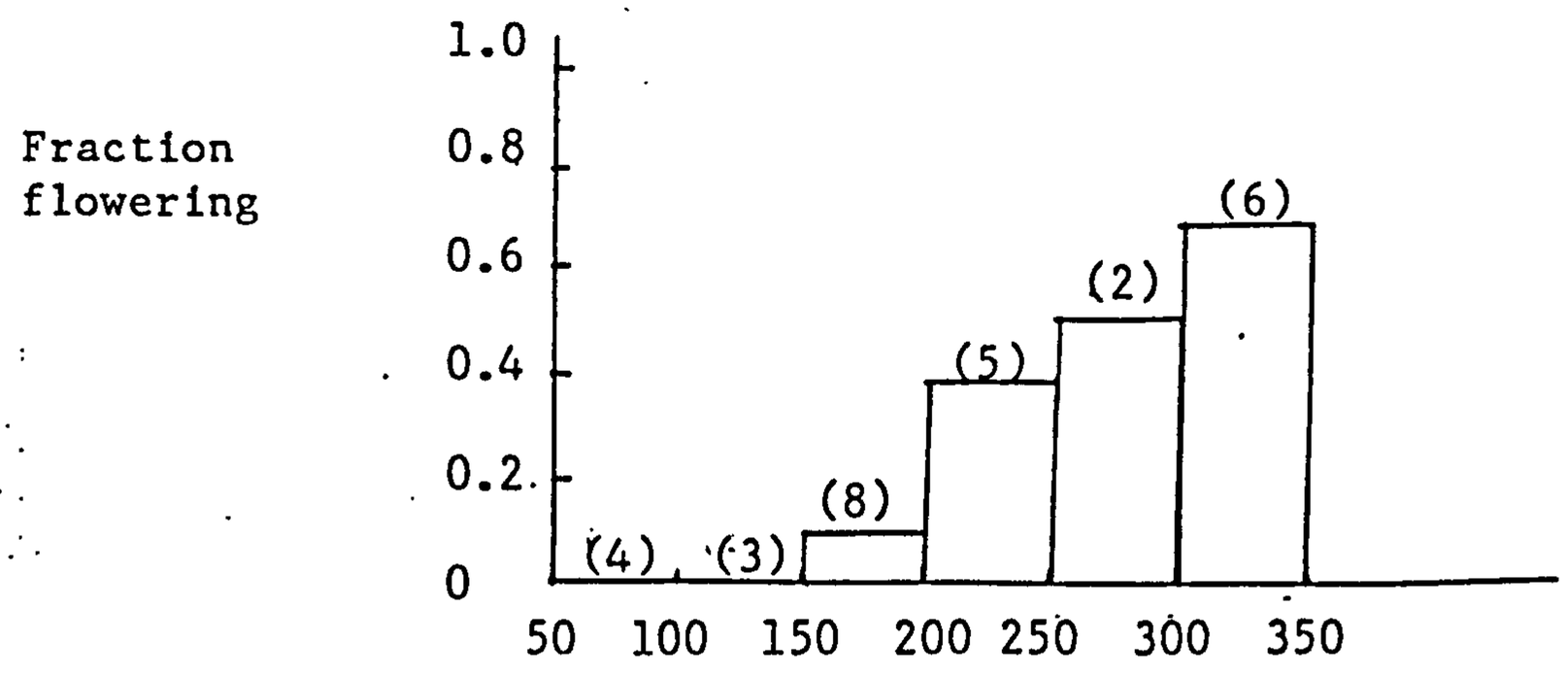


Figure 6.5

Fraction of R. repens plants flowering in each ramet density class (n in brackets) for the submerged plants in experiment 3.

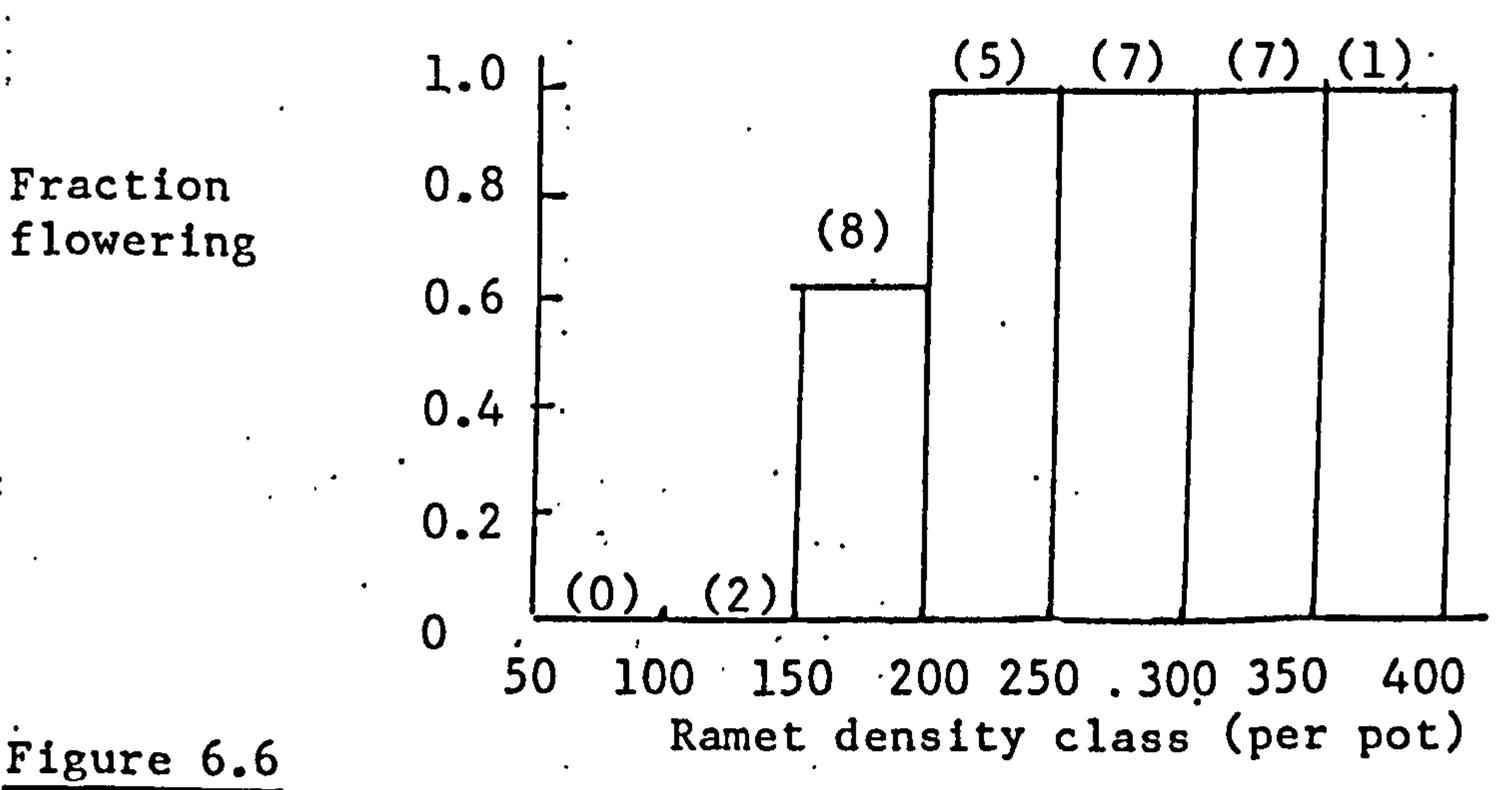


Figure 6.6

Fraction of R. repens plants flowering in each ramet density class (n in brackets) for the control plants in experiment 3.

In the controls all plants with a ramet density above 200/pot flowered and so did several plants with lower densities but none with densities of less than 150 ramets (Figure 6.6). All plants above a ramet density of 170/pot flowered and only 1 with a density below this flowered. In the submerged plants the probability of flowering never reaches 1 and is always less than for control plants at the same density. Flowering and density are not as closely linked in the submergence treatment as in the control treatment.

Ramet density is a good predictor of flowering behaviour and unlike total dry weight it is applicable independent of site in the submerged treatment. The reduction in flowering found in the submergence treatments of the Port Meadow non-submerged and Open University sites is not due to a reduction in ramet density (Table 6.9) but to the reduction in the probability of flowering at a particular ramet density (Figures 6.5 & 6.6). The lower ramet density in the Port Meadow submerged site plants under the submergence treatment would also contribute to the reduced flowering in these plants (Table 6.9).

6.5 The number of flowers per plant

The above results are concerned with flowering or not flowering but some plants had two flowers while others had seven. The number of flowers per (flowering) plant is significantly reduced by submergence in both the Port Meadow non-submerged and the Open University site plants (Table 6.6). Is the number of flowers per plant controlled by either total dry weight or ramet density or some other factor?

There is a trend towards increased number of flowers per plant with

Table 6.9

Density of ramets (per pot means) at harvest for R. repens in experiment 3. Plants were collected from the three sites in January 1983 and subjected to a submergence or control treatment and harvested in August 1983 (n= 10).

Treatment	Site		
	Port Meadow submerged	Port Meadow non-submerged	Open University
Control	193^{b**}	278^{c}	238^{bc}
Submergence	129^{a}	242^{bc}	231^{bc}

Pooled S.E. = 19.2
Anova: Site $p<0.001$;Treatment $p<0.05$;Interaction n.s.
** different superscript means significantly different at $p<0.05$ using pooled S.E. in t-test (see Mead and Curnow, 1983).

increasing density in the control plants (Figure 6.7) but in the submerged plants the relationship is not clear (Figure 6.8); this is possibly due to few data points.

In the control plants increased total dry weight up to 100g results in increased number of flowers per plant (Figure 6.9) but this relationship breaks down above this point. When the sites are studied individually (Table 6.10) the site-dependent nature of the response can be seen. Overall flower number per plant increases with increasing dry weight in the control plants; although this is not clearly seen in the Port Meadow non-submerged site plants. In the submergence treatment the relationship between these variables is different from the controls with generally fewer flowers/plant at the same total dry weight class (Figure 6.10)

6.6 Discussion

These results provide further evidence to support genetic differentiation between the three site populations (Chapter 5). However, these results show the Port Meadow submerged site plants to be different from the plants from the other two sites. Under controlled conditions they show no delay in flowering and lower probability of flowering in non-submerged conditions. Although the probability of flowering is reduced in the submergence treatment the reduction is less then for the other sites and there is no significant reduction in the number of flowers per plant following submergence.

Flowering in R. repens plants has been shown here to be related to total dry weight. Werner (1975) found that rosette diameter (as an index of

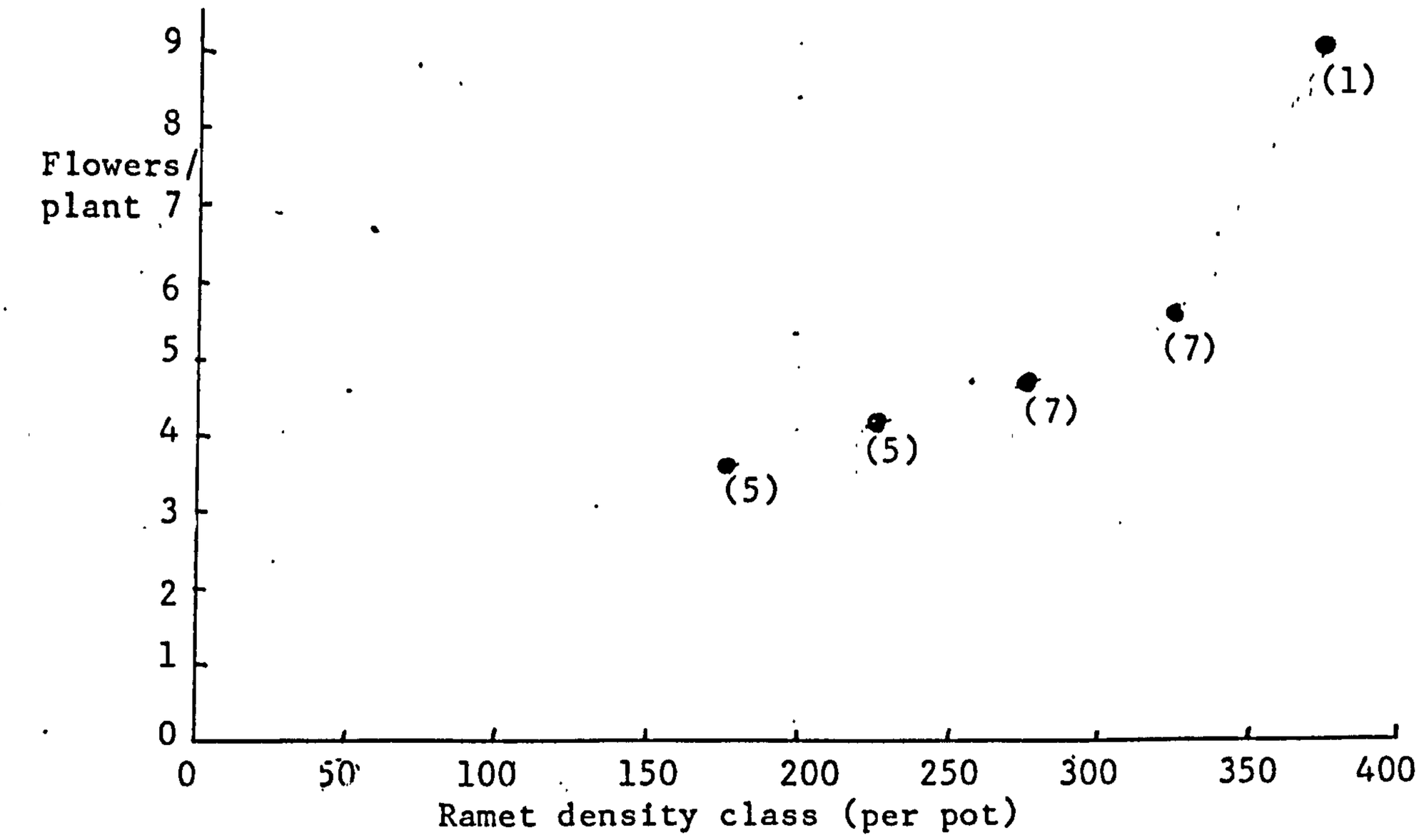


Figure 6.7

The mean number of flowers per plant for the R. repens plants in the control treatment of experiment 3 plotted against ramet density class (class mid-points plotted).

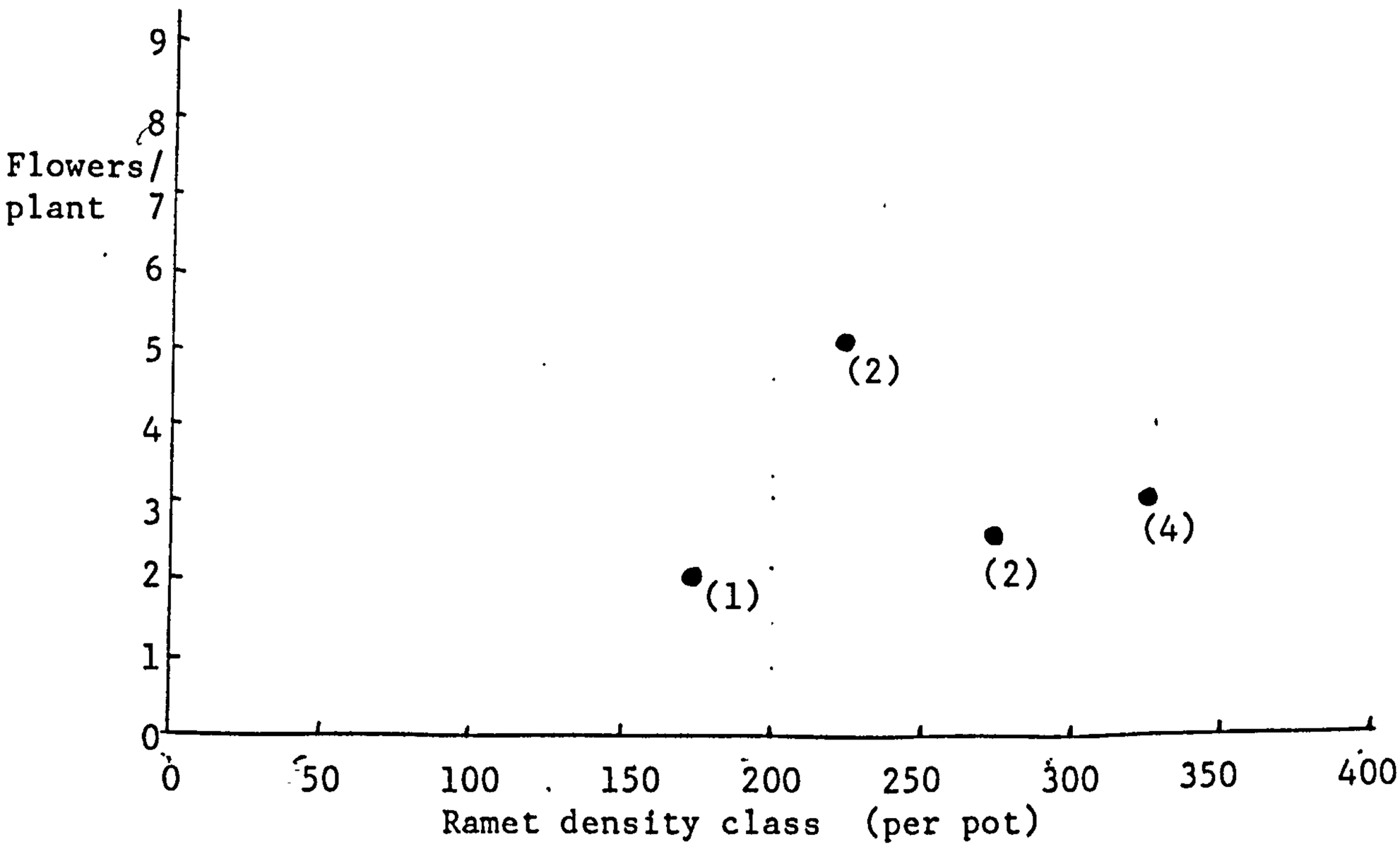


Figure 6.8

The mean number of flowers per plant for R. repens plants in the submergence treatment of experiment 3 plotted against ramet density class (class mid-points plotted, n in brackets).

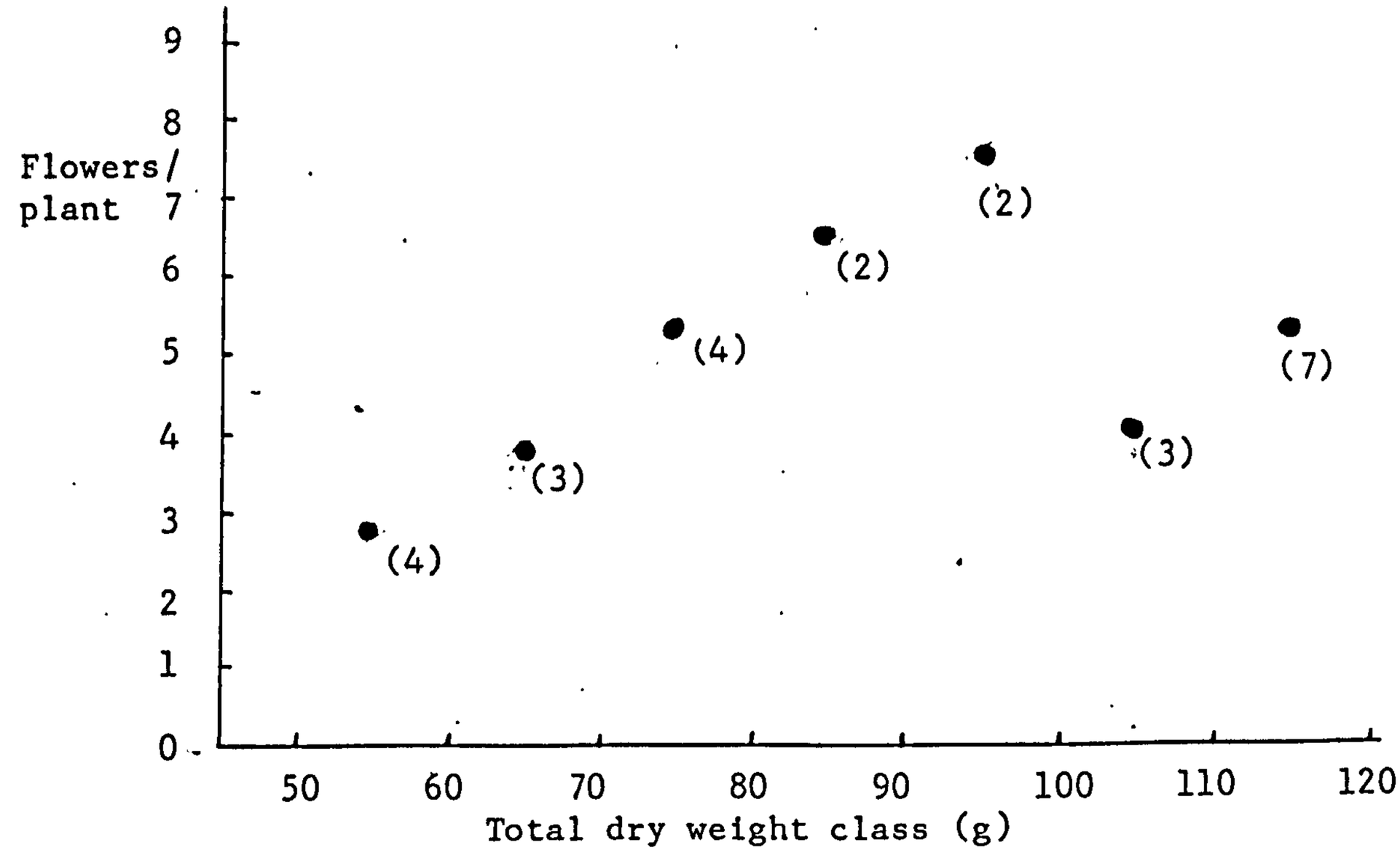


Figure 6.9

The mean number of flowers per plant for the R. repens plants in the control treatment of experiment 3 plotted against total dry weight class (class mid-points plotted, n in brackets).

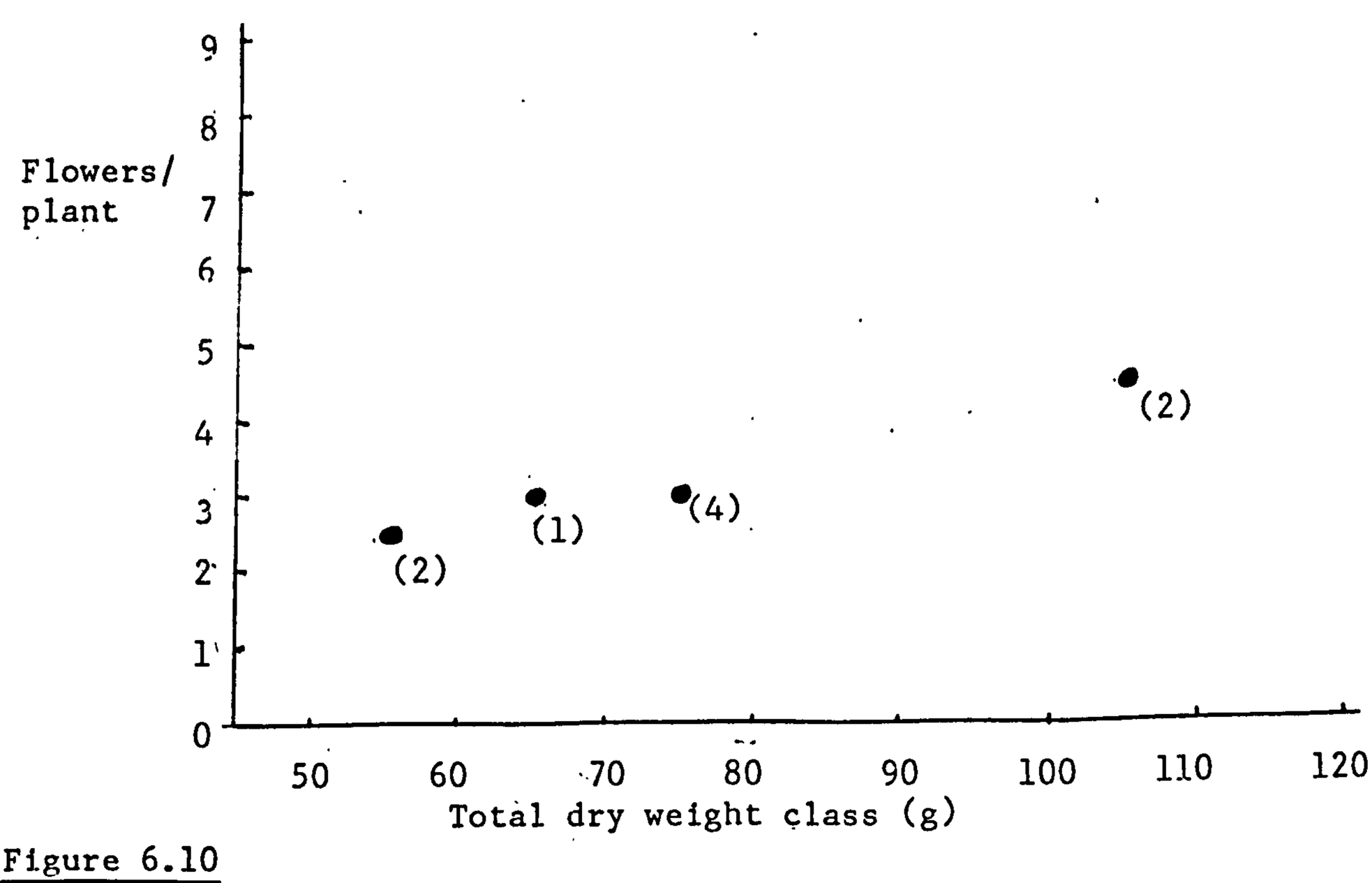


Figure 6.10

The mean number of flowers per plant for R. repens plants in the submergence treatment of experiment 3 plotted against total dry weight class (class mid-points plotted, n in brackets).

Table 6.10

Number of flowers (mean and S.E.) per *R. repens* plant by site and total dry weight for the control treatment in experiment 3. Plants were collected from the three sites during January 1983 and harvested during August 1983.

Total dry weight (g)	Site: Port Meadow submerged	n	Port Meadow non-submerged	n	Open University	n
50-69	3.5 (0.5)	2	--	0	3.0 (0.5)	5
70-89	5.0	1	4.0 (0.0)	2	7.0 (0.6)	3
90-109	6.0	1	4.0 (0.0)	3	9.0	1
110-120	7.0 (0.0)	2	4.6 (0.3)	5	--	0

plant size) was a critical determinant of the flowering behaviour of the monocarpic perennial Dipsacus fullonum; plants with large diameters had a greater probability of flowering. Size-dependent flowering has been shown for several other monocarpic perennials (Baskin and Baskin, 1979; Reinartz, 1984a). Flowering in several clonal perennials has been found to be dependent on ramet size (Barkham, 1980; Pitelka et al, 1985), with larger ramets more likely to flower.

Ramet size is very often inversely proportional to ramet density (Hutchings, 1979; and see Chapter 6). This implies that ramet density and flowering would be expected to be related inversely. However, ramet density was strongly positively correlated with flowering. This difference can be explained by the fact that the ramets within a single plant in experiment 3 were all attached and therefore physiologically linked. The importance of this difference can be seen with density dependent mortality. This is found between clones but not found within the ramets of a single attached clone (Hutchings, 1979; Kays and Harper, 1974).

Support for the results presented here comes from Williams (1975). His clonal perennial model predicts that increased ramet density within an attached clone will result in an increased emphasis on sexual reproduction.

Going back to the initial question of a flowering strategy in response to seasonal submergence, the above results suggest that submergence reduces the probability of R. repens plants flowering. Submergence apparently affects the relationship between density and flowering so as to reduce the probability of flowering at a particular density. The reason for this may be related to the 'resource costs' of flowering.

Pitelka et al (1985) concluded that for the clonal perennial Clintonia borealis resource costs (based on percentage dry weight) for the production of a stolon were much less than those required to produce a peduncle and fruits. Cessation of flowering would then reduce the resource burden of a 'stressed' previously submerged plant.

From the above discussion the situation in the 'field with unattached ramets will probably be very different from the results from clones made up of attached ramets.

6.7 Summary

1. There is evidence that submergence results in a delay in flowering in R. repens plants but this varies with site of origin.

2. Submergence reduces the probability of flowering in R. repens.

3. The results suggest that flowering in R. repens is related to both ramet density and total dry weight. Increases in both increase the probability of flowering.

4. The reduction in flowering in submerged plants is associated with a change in the relationship between flowering probability and total dry weight, and flowering probability and ramet density.

5. The number of flowers/plant is also related to ramet density and total dry weight. The relationship between the number of flowers/plant and ramet density breaks down after a submergence treatment.

Chapter 7

Growth Form and Submergence in Ranunculus repens

"..genets behave like the prudent farmer and do not crowd their ramets to the point at which mortality prematurely reaps some of the harvest.."

(Silvertown, 1982:134)

7.1 Introduction

In recent years there has been considerable interest in plant growth form (e.g. Harper, 1977; Halle et al, 1978; Harper and Bell, 1979; Bell, 1974). Attempts have been made to describe the growth form of particular plants in terms of a few simple rules (e.g. Maillette, 1982a; 1982b with Betula pendula). Much of this interest has been associated with the growth form strategies shown by clonal perennial plants (e.g. Bell, 1974; 1979; Bell et al, 1979; Bell and Tomlinson, 1980; Lovett Doust, 1981a; 1981b; Hartnett and Bazzaz, 1985b).

Lovett Doust (1981a) and Harper (1981) have introduced the terms phalanx and guerilla to describe the patterns of growth form of clonal perennials (see also Clegg, 1978). The phalanx growth form describes a genet consisting of a dense mass of tightly packed ramets making little contact with other plants. The guerilla growth form produces a loosely packed genet, making large numbers of contacts with other plants. The terms are used relatively and plants can be placed on a phalanx-guerilla growth form continuum (Bulow-Olsen et al, 1984)

Lovett Doust (1981a) suggests that the distances between ramets on a stolon (the stolon internode lengths) describe the relative position of a clone on this growth form continuum. The greater the stolon internode lengths the more guerilla-like in growth form is the clone. Lovett Doust (1981a) related increases in allocation of dry weight to stolons with increases in stolon internode lengths in Ranunculus repens.

Genetically based differences with respect to stolon internode lengths have been shown between adjacent populations of the same species of clonal perennial (Lovett Doust, 1981a; Burdon, 1980; Aston and Bradshaw, 1966). Lovett Doust (1981a) has also shown that stolon internode lengths are site specific, environmentally plastic and that the degree of plasticity varies from population to population.

This chapter concentrates on the growth form strategies of Ranunculus repens genets and any growth form changes that occur due to seasonal submergence. The following questions were asked:

1. Does the growth form of R. repens respond to submergence in a tactical sense?

2. Is there evidence for genetic differentiation between populations based on differences in growth form and the response of growth form to submergence?

3. Can an overall growth form strategy in relation to submergence be put forward?

The results in this chapter are based on the assumption that stolon internode lengths are an important descriptor of plant growth form in

R. repens, as postulated by Harper (1981) and Lovett Doust (1981a). This character was measured as opposed to other possible descriptors, such as branch angle (Bell and Tomlinson, 1980), the density of apices (Bulow-Olsen et al, 1984) and the demography of buds (Maillette, 1982a; 1982b). Other growth form characteristics, such as stolon length were also studied.

7.2 Field Results

Stolon internode lengths were measured in plants from the three field sites during June 1983 (see Appendix 1 and section 2.4). Stolon internode lengths differed considerably between sites but very little within sites (Table 7.1). Plants from the Open University site have much shorter stolon internode lengths than plants from the Port Meadow sites, with the submerged site plants having the longer (Table 7.1). There is evidence here to suggest that seasonal submergence has resulted in longer stolon internode lengths. This is either genetically or tactically based, or both, resulting in a more guerilla-like growth form.

Plants from the three sites do not differ in terms of the number of stolons and ramets/genet (Table 7.2). It is therefore not suprising, following the stolon internode length differences, that individual stolon lengths vary (Table 7.2). However, plants from the Port Meadow sites do not differ significantly but these have stolons that are significantly longer than stolons of Open University site plants (Table 7.1).

The next step was to separate environmentally and genetically based

Table 7.1

Lengths of stolon internodes (mean and S.E.) and of individual stolons (mean and S.E.) for *R. repens* plants collected in the three field sites in June 1983.

Site	Stolon Internode length/plant (cm)	n	Individual Stolon length (mm)	n
Port Meadow submerged	11.4 (0.3)^{a**}	31	292.6.(53.2)^{a}	16
Port Meadow non-submerged	9.8 (0.3)^{b}	36	253.1 (68.5)^{a}	16
Open University	6.4 (0.1)^{c}	21	151.9 (22.3)^{b}	18

** as in all tables different superscript means significantly different at $p<0.5$ (t-test).

Table 7.2

The number of stolons and ramets (per plant, mean and S.E.) borne by *R. repens* plants collected from the three field sites in June 1983 (n= 10).

Site	Stolons/plant	Ramets/plant
Port Meadow submerged	1.6 (0.2)^{a}	4.6 (0.6)^{a}
Port Meadow non-submerged	1.6 (0.3)^{a}	4.3 (0.4)^{a}
Open University	1.8 (0.2)^{a}	4.3 (0.4)^{a}

differences in growth form using experimental data.

7.3 Experimental results

In the following experiment (details in section 2.4; experiment 3) rosettes of R. repens were collected from the three study sites (Appendix 1) and transplanted into a transplant garden. They were then grown under submerged or non-submerged (control) treatments.

With stolon internode lengths the transplanted plants show significant effects of site of origin, submergence and an interaction between these factors (Table 7.3). Plants from both the Port Meadow sites show an increase in stolon internode length with submergence, with the submerged site plants showing the greater increase. In contrast, the Open University site plants show a decrease in stolon internode length with submergence.

In the control treatment the stolon internode lengths in the Port Meadow site plants are not significantly different but in the submergence treatment the submerged site plants have much longer stolon internode lengths (Table 7.3). Based on stolon internode lengths the relative position of the plants on the phalanx-guerilla growth form continuum is altered by the submergence treatment.

Total length of stolon per genet was significantly affected by site of origin and by the submergence treatment, which interacted with site of origin (Table 7.4). However, only the Port Meadow submerged site plants show a significant change in total stolon length with submergence.

Table 7.3

Stolon internode lengths (cm, mean/plant) at harvest for pot grown R. repens plants collected from the three field sites in January 1983 and subjected to a submergence or control treatment and harvested in August 1983 (n= 10).

Treatment	Site		
	Port Meadow submerged	Port Meadow non-submerged	Open University
Control	9.5a**	10.4a	12.1b
Submergence	19.5c	12.9b	10.3a

Pooled S.E.= 0.35.
Anova: Site p<0.001;Treatment p<0.001;Interaction p<0.001.
** different superscript means significantly different at p<0.05 using pooled S.E. in t-test (see Mead and Curnow, 1983).

Table 7.4

Total stolon length (m, mean/plant) at harvest for pot grown R. repens plants collected from the three field sites in January 1983 and subjected to a submergence or control treatment and harvested in August 1983 (n= 10).

Treatment	Site		
	Port Meadow submerged	Port Meadow non-submerged	Open University
Control	17.8a**	28.8bc	28.3bc
Submergence	24.8b	31.0c	23.5b

Pooled S.E.= 1.93
Anova: Site p<0.001;Treatment n.s;Interaction p<0.05
** different superscript means significantly different at p<0.05 using pooled S.E. in the t-test (see Mead and Curnow, 1983).

In the control treatment the Port Meadow submerged site plants had much shorter total stolon lengths compared with the other two sites (Table 7.4). However, in the submergence treatment the Port Meadow submerged site plants and the Open University site plants are not significantly different and the Port Meadow non-submerged site plants have significantly longer total stolon lengths per genet (Table 7.4).

Another variable to consider for clonal perennials is the total number of ramets per genet. In this case, as the plants were grown in identical pots, this is a measure of ramet density. The number of ramets per genet was quite variable, both within and between sites and treatments, with as much as a three fold variation within a single site-treatment group.

Overall there is a significant effect of site of origin and submergence treatment on the number of ramets/genet (Table 7.5). However, only the Port Meadow submerged site plants show a significant change in the number of ramets/genet with the submergence treatment (Table 7.5). Within both treatments the Port Meadow submerged site plants have the lowest, or equal lowest, number of ramets/genet and the other two sites are not significantly different within both treatments (Table 7.5).

Mean individual ramet dry weight, like all the previous variables shows a significant effect of site of origin (Table 7.6) and the submergence treatment effect interacts with the site of origin. Plants from both Port Meadow sites show significant changes in individual ramet dry weight (Table 7.6). However, the changes are in opposite directions.

Under the control treatment there is no significant difference between plants from the two Port Meadow sites but both are significantly greater

Table 7.5

Number of ramets/plant (mean) at harvest for pot grown *R. repens* plants collected from the three field sites in January 1983 and subjected to a submergence or control treatment and harvested in August 1983 (n= 10).

Treatment	Site		
	Port Meadow submerged	Port Meadow non-submerged	Open University
Control	193^{b**}	278^{c}	238^{bc}
Submergence	129^{a}	242^{bc}	231^{bc}

Pooled S.E.= 19.2
Anova: Site $p<0.001$;Treatment $p<0.05$;Interaction n.s.
** different superscript means significantly different at $p<0.05$ using pooled S.E. in t-test (see Mead and Curnow, 1983).

Table 7.6

Dry weights of individual ramets/plant (g, mean) at harvest for pot grown *R. repens* plants collected from the three field sites in January 1983 and subjected to a submergence or control treatment and harvested in August 1983 (n= 10).

Treatment	Site		
	Port Meadow submerged	Port Meadow non-submerged	Open University
Control	0.38^{c**}	0.37^{c}	0.26^{b}
Submergence	0.51^{d}	0.23^{a}	0.26^{b}

Pooled S.E.= 0.0095
Anova: Site $p<0.001$;Treatment n.s;Interaction $p<0.001$.
** different superscript means significantly different at $p<0.05$ using pooled S.E. in t-test (see Mead and Curnow, 1983).

than the Open University site plants (Table 7.6). Under the submergence treatment individual ramet dry weights are much greater in the Port Meadow submerged site plants compared with the other two sites, which did differ significantly (Table 7.6). The submergence treatment, again, changes the relationship of the three sites based on a variable of clonal growth.

Overall there is a highly significant negative correlation between the number of ramets/genet (Table 7.5) and individual ramet dry weight (Table 7.6) ($r=-0.58$; $p<0.001$). Stolon internode lengths (Table 7.2) are also significantly negatively correlated with the number of ramets/genet ($r=-0.58$; $p<0.001$).

7.4 Discussion

The transplant experiment shows genetic differences between the three site populations with respect to stolon internode lengths (Table 7.2). This supports the findings of genetically based differences in stolon internode lengths in this species (Lovett Doust, 1981a) and in two other stoloniferous clonal perennials; Trifolium repens (Burdon, 1980) and Agrostis stolonifera (Aston and Bradshaw, 1966). These findings were all made between adjacent populations as at the Port Meadow sites.

The populations can also be separated on their tactical changes in stolon internode lengths in response to submergence (Table 7.2). This was also found by Lovett Doust (1981a) in adjacent woodland and grassland populations of R. repens. Lovett Doust's (1981a) woodland population showed a more guerilla-like strategy (i.e. longer stolon internode lengths) relative to the grassland population and she suggests

that this might be related to an increased probability of sampling a sunfleck in the woodland. The Port Meadow site populations show a more guerilla-like growth form in response to submergence and this is also shown in the field results (Table 7.1). This is perhaps related to the increased probability of sampling more favourable non-submerged conditions.

In Chapter 5 Ginzo and Lovell's (1973a; 1973b) proposed 'getting away' strategy for R. repens in response to decreasing nitrogen supply was discussed. Under these conditions R. repens produced fewer, longer stolons with reduced dry weight/cm of stolon length (see Chapter 8). This increases the probability that a ramet will be placed away from the unfavourable parent site. The increase in total stolon length (Table 7.4) in the Port Meadow submerged site plants may be part of this strategy, along with changes in the stolon internode lengths.

Individual stolon lengths were not measured in experiment 3. The field results (Table 7.1) show the production of longer individual stolons in submerged conditions. In an earlier experiment (experiment 2 - section 2.4) plants from the Open University site under the 4-week submergence treatment produced fewer stolons which were not significantly different in individual length from those of control (non-submerged) plants (Table 7.7). More research is needed to see if this is a part of a general strategy.

Another example of this 'getting away' from an unfavourable site is suggested by Hartnett and Bazzaz (1983) who found that severing of the rhizomes connecting a young ramet of Solidago canadensis to its parent, resulted in the ramet producing fewer, longer rhizomes. They liken the result to intense competition depleting resources, but this is not in

Table 7.7

The number of stolons, individual stolon length and total stolon length (mean and S.E.) for *R. repens* plants at harvest grown in experiment 2.

Treatment	Stolons /plant	Individual stolon length (cm)	Total stolon length/plant (cm)	n
Controls	6.1 (0.8)a**	42.3 (9.3)a	257.7 (47.7)a	11
4-week submerged	2.2 (0.2)b	34.4 (7.4)a	74.6 (14.6)b	12
8-week submerged	1.5 (0.2)c	6.3 (1.5)b	9.5 (2.8)c	6

** different superscript means significantly different at $p<0.05$ (t-test).

agreement with the results of Bradbury and Hofstra (1976) who found that Solidago canadensis plants growing in a closed site produced shorter rhizomes than those in an open site.

This contradiction may be explicable in the differential response of clonal perennials to nutrient and competitive 'stress' (see section 1.8). Decreasing nutrients generally results in an increase in emphasis on stolons or rhizomes (Ginzo and Lovell, 1973a; 1973b; Ogden, 1974; Andel and Vera, 1977) whereas increasing density results in decreased emphasis on stolons or rhizomes (Ogden, 1974; Thomas and Dale, 1974; Holler and Abrahamsom, 1977).

This appears counterintuitive and is certainly different from the results for sexual reproduction, which is decreased or unchanged by nutrient and competitive stress (e.g. Hiroi and Monsi, 1966; Ogden, 1974; Snell and Burch, 1975; Raynal and Bazzaz, 1975; Pemadasa, 1976; Andel and Vera, 1977; Lovett Doust, 1980; Steen, 1984). However, Williams (1975) predicts from a cost-benefit model of clonal growth that increased competitive stress will result in a decreased emphasis on rhizomes or stolons.

There is evidence that clonal perennials regulate their densities and therefore avoid density dependent mortality (Kays and Harper, 1974; Hutchings, 1979; Pitelka, 1984). Harper (1981) considers that this density control is brought about through regulation of inter-ramet distances. The results reported here support this hypothesis, as a significant negative relationship between stolon internode lengths and density was found. However, it is not suprising that stolon internode lengths do not explain perfectly variations in the ramet density because other factors, such as branching angle and the rules of ramet production

will also influence spatial arrangement (Hutchings, 1979; Bell and Tomlinson, 1980)

As with other studies individual ramet dry weight is negatively correlated with ramet density (Matthews and Westlake, 1969; Hutchings, 1979). There is, however, much evidence to suggest that individual ramet weights and density do not follow the typical self-thinning relationship (Yoda et al, 1963; White, 1980) and therefore do not show density dependent mortality (Hutchings, 1979). Individual ramet weight has been found to be of critical importance in the survival and flowering of ramets (Pitelka et al, 1985; and see Chapter 5), and therefore the dynamics of clonal perennials.

Clearly R. repens can make tactical changes in growth following submergence and there is evidence for genetic differentiation based on these changes. Plants from both the Port Meadow sites show evidence of a 'getting away' strategy similar to one that has been proposed for other clonal perennials (Ginzo and Lovell, 1973a 1973b; Hartnett and Bazzaz, 1983). Plants from the Open University site appear to show a different submergence strategy. Other workers have found evidence for differing strategies between populations of a single species (Reinartz, 1984; Rochow, 1970; Mooney and Billings, 1961; Kingsbury et al, 1976; Douglas, 1981).

7.5 Summary

1. Field data show that R. repens plants from a submerged site have a more guerilla-like growth form in terms of stolon internode lengths than those from non-submerged sites.

2. The experimental results show this may be due to tactical changes and therefore not genetically fixed.

3. In agreement with other research, different populations of R. repens show differential plasticity with respect to stolon internode lengths.

4. R. repens plants from different populations can also show contrasting changes in stolon internode lengths with submergence.

5. The results for the two Port Meadow site populations can be interpreted as part of a strategy for 'getting away' from an unfavourable site.

Chapter 8

Changes in the Dry Weight Per Unit Length of Stolons and Petioles with Submergence in Ranunculus repens

"..stolons confer upon R. repens a kind of trial-and-error policy in the exploration of the habitat.."

(Ginzo and Lovell, 1973b)

8.1 Introduction

Reductions in the dry weight per unit length in stolons of R. repens have been related to reductions in total dry weight resulting from a limited nitrogen supply (Ginzo and Lovell, 1973a). Submerged plants of R. repens can have reduced resources compared to non-submerged plants (Chapter 3) and so it is of interest to see whether or not submergence stress influences dry weight per unit length as does nitrogen stress.

Stolons play an important role in the maintenance of R. repens populations (Sarukhan and Gadgil, 1973; Soane and Watkinson, 1979). However, stolons usually appear after submergence has taken place and so changes in dry weight distributions will not be as a result of submergence per se. Stolon length can be judged as important because it is a determinant of the extent of vegetative spread.

Petioles were also included in this study because they are known to respond to submergence by elongation (see section 1.8), and it is of interest to see if this involves changes in the amount of dry matter per

unit length of petiole, especially considering the reduced total dry weight of submerged plants. Observations of the petioles of submerged plants suggest that these are thinner and less rigid than non-submerged counterparts (S.J.Smith pers. obs.). Petiole length is of particular importance in terms of submergence in that it determines whether or not a petiole will reach the surface of the water and the importance of this was shown in experiment 1 (Chapter 3).

Dry weight per unit length can be used as an index of the distribution of dry weight in these structures and can be considered as ecologically meaningful.

Several detailed questions are of interest here:

1. Does submergence result in differences in the distributions of the allocated material in petioles and stolons?

2. If differences are present, do they persist after submergence and are they long term?

3. Is there evidence for genetic differentiation between populations of R. repens with respect to dry weight distributions within stolons and petioles and the changes that occur following submergence?

8.2 Experimental Results

Straight line relationships between dry weight and length for both stolons and petioles were found under all the conditions studied and so

mean values of dry weight per unit length will be used throughout this chapter.

8.2.1 Petioles and dry weight per unit length

Experiment 1 involved three treatments. Air grown for 13 weeks; submerged for 5 weeks and then air grown for 8 weeks; 13 weeks submerged (for details see section 2.4). The results show that the distribution of dry weight per unit length in petioles is clearly affected by submergence (Table 8.1). The 13 week submerged rosettes have about 20% of the dry matter per cm relative to the air grown controls. The same weight of petiole in the submerged plants would be five times longer than the same weight of petioles from control plants.

The 5 week submerged rosettes have a dry weight per mm which is close to that of the control plants, containing about 3/4 of the material that the same length of control plant petiole has (Table 8.1). Clearly the 5 week submergence treatment has had effects on dry matter distribution even after 8 weeks of growth in air (Table 8.1).

Experiment 3 involved the submergence or the growing in air of rosettes transplanted from the three study sites (see Chapter 2). The results show that submergence results in reduced dry weight per mm of petiole independent of site of origin (Table 8.2). With the exception of the controls from the Port Meadow submerged site, there is a remarkable consistency in dry weight per mm within each treatment (Table 8.2). The submergence treatment petioles show a 20 to 30% reduction in dry weight per mm which is reflected in $1\frac{1}{4}$ - $1\frac{1}{2}$ times the petiole length for the same weight of petioles as the control plants (Table 8.2). The higher

Table 8.1

Dry weight per mm of petiole length (mean and S.E. per plant) for *R. repens* plants grown in experiment 1.

Treatment	Dry weight/mm of petiole length (mg/mm x10-3)	n
Controls	29.0 (1.36)a**	12
5-week submerged	21.6 (0.66)b	12
13-week submerged	6.0 (0.84)c	12

** different superscript means significantly different at $p<0.05$ (t-test).

Table 8.2

Dry weight per mm of petiole length at harvest (mg/mm, per plant, means) for *R. repens* plant collected during January 1983 from the three study sites and subjected to a submergence or control treatment and harvested during August 1983 (experiment 3, n= 10).

Treatment	Site		
	Port Meadow submerged	Port Meadow non-submerged	Open University
Control	0.323a**	0.271b	0.274b
Submergence	0.224c	0.215c	0.214c

Pooled S.E.= 0.012
Anova: Site 0.05;Treatment $p<0.001$;Interaction n.s.
** different superscript means significantly different at $p<0.05$ using pooled S.E. in t-test (see Mead and Curnow, 1983).

value of dry weight per mm of petiole length for the Port Meadow submerged site plants is more evidence for genetic differentiation between the populations. The submerged plants were submerged in February and harvested in August so submergence is having a long term effect on the dry weight per unit length of petioles.

Field data, collected from the three study sites (see Chapter 2), shows an interesting picture for petiole dry weight per unit length (Table 8.3). With the exception of June, the Port Meadow submerged site petioles showed lower dry weight per mm compared with the Port Meadow non-submerged site petioles (Table 8.3; Figure 8.1). In February the Open University site petioles showed a low dry weight per mm that was not significantly different from the Port Meadow submerged site petioles. However, in March the level had risen to be greater than both Port Meadow sites (Table 8.3).

From February to April inclusive the Port Meadow non-submerged site petioles had about 1.5 times the dry matter per mm of the petioles of the Port Meadow submerged site (Table 8.3; Figure 8.1), whereas in May the Port Meadow non-submerged site petioles contained about 2.5 times the dry matter per mm of the Port Meadow submerged site petioles. In June the picture is the reverse of the earlier position with the Port Meadow submerged site petioles having about 1.5 times the dry matter in the Port Meadow non-submerged site petioles.

During the study period the Port Meadow non-submerged site petioles show a larger range in dry weight per mm compared with the Port Meadow submerged site petioles (Figure 8.1). However, a major difference between the two patterns of petiole dry weight distribution is the decrease in May at the Port Meadow submerged site which was followed by

Table 8.3

Dry weight per mm of petiole length (mg/mm, per plant means and S.E.) for R. repens plants collected from the three field sites from February to June 1983 (n = 10 to 20).

Month	Site		
	Port Meadow submerged	Port Meadow non-submerged	Open University
February	0.149 (0.009)^{b**}	0.223 (0.008)^{de}	0.167 (0.005)^{b}
March	0.108 (0.006)^{a}	0.176 (0.012)^{bc}	0.225 (0.019)^{de}
April	0.247 (0.018)^{e}	0.360 (0.011)^{g}	n/a
May	0.186 (0.021)^{bcd}	0.483 (0.032)^{h}	n/a
June	0.306 (0.020)^{f}	0.217 (0.022)^{cde}	n/a

** different superscript means significantly different at $p<0.05$ (t-test).
n/a = no data collected.

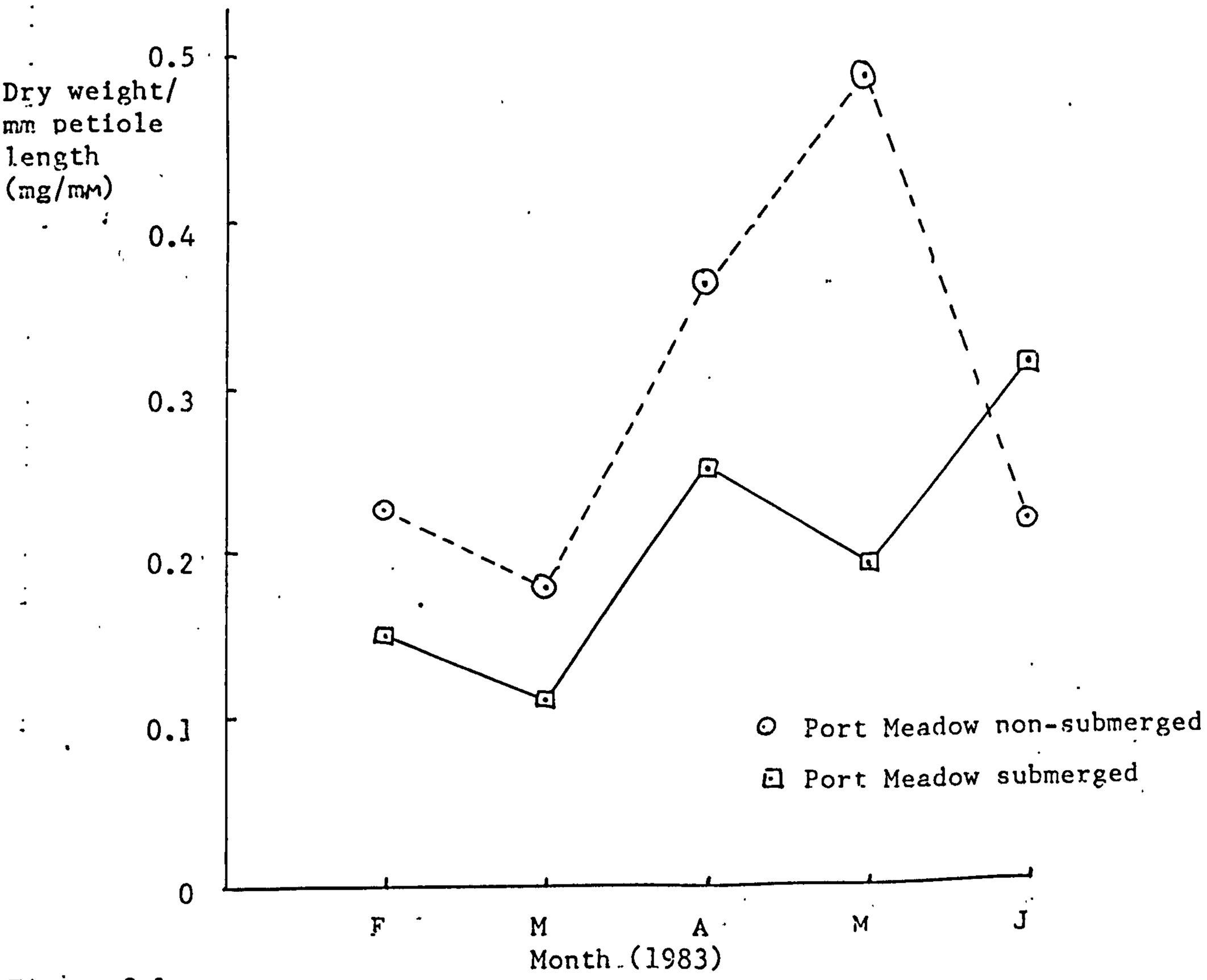


Figure 8.1

The dry weight per mm of petiole length for R. repens plants collected from the two sites from February to June 1983 (see Table 8.3).

an increase in June (Figure 8.1).

It is interesting to note that the pattern of changes in dry weight per unit length in petioles in both Port Meadow sites plants (Figure 8.1) mirrors the changes in average dry weight per genet (Figure 8.2).

8.2.2 Stolons and dry weight per unit length

Experiment 2 involved three treatments. Twelve weeks air grown (controls), four weeks submergence followed by eight weeks growing in air and eight weeks submergence followed by four weeks growing in air (full details in section 2.4).

The results from experiment 2 show that stolons of the previously submerged rosettes have lower dry weight per mm than stolons from control rosettes (Table 8.4). Stolons from plants in the 8 week submergence treatment have about three quarters of the dry weight per mm of the stolons from control plants. Stolons from the 4 week submerged plants have about half of the dry weight per mm of control plant stolons (Table 8.4). However, the 4 week and 8 week submerged plants do not show significantly different levels of dry weight per mm for stolons. Clearly, submergence can have long term (eight weeks post-submergence) effects on the distribution of dry weight in stolons.

The results from experiment 3 (see above and section 2.4 for details) for stolon dry weight distribution are quite complex. Plants collected from the Open University site do not show any reduction in dry weight per mm 5 months after submergence (Table 8.5). However, both Port Meadow submerged site and Port Meadow non-submerged site plants show a

Table 8.4

Dry weight per mm of stolon length (mean and S.E. per plant) for *R. repens* plants grown in experiment 2.

Treatment	Dry weight/mm stolon length (mg/mm)	n
Controls	5.4 (0.36)[a]	11
4-week submerged	3.9 (0.23)[b]	12
8-week submerged	3.0 (0.37)[b]	6

Table 8.5

Dry weight per mm of stolon length (mean per plant) for *R. repens* plants collected from the three field sites during January 1983 and subjected to either a submergence or control and harvested in August 1983 (n= 10).

Treatment	Site		
	Port Meadow submerged	Port Meadow non-submerged	Open University
Control	1.33a**	1.16b	0.95c
Submergence	0.88d	0.70e	0.99c

Pooled S.E. = 0.08
Anova: Site $p<0.001$; Treatment $p<0.001$; Interaction $p<0.001$.
** different superscript means significantly different at $p<0.05$ using pooled S.E. in t-test (see Mead and Curnow, 1983).

Table 8.6

Dry weight per mm of stolon length (mean and S.E. per plant) for *R. repens* plants collected from the three field sites during June 1983 (n= 10).

Site	Dry weight per mm of stolon length (mg/mm)
Port Meadow submerged	0.55 (0.03)a**
Port Meadow non-submerged	0.38 (0.04)b
Open University	0.60 (0.03)a

** different superscript means significantly different at $p<0.05$ (t-test).

reduction in dry weight per mm in stolons following submergence (Table 8.5). The Port Meadow submerged site plants show the lesser reduction with about a one-third reduction in dry weight per mm whereas the Port Meadow non-submerged site plants show about a two-fifths reduction in dry weight per mm (Table 8.5). Hence, not only can submergence affect the dry weight distribution in stolons five months or so after the event but this effect is also dependent on the site of origin of the plants.

The field results (from the three study sites; see section 2.4 and Appendix 1) for stolon dry weight distributions for June show that stolons at the Port Meadow non-submerged site have less dry weight per mm than at the Open University and Port Meadow submerged sites (Table 8.6). The dry weight per unit length for stolons of the latter two sites are not significantly different (Table 8.6). The Port Meadow non-submerged site stolons have about one-third less dry matter per mm than stolons of the other two sites (Table 8.6).

These results do not agree with the results found under controlled conditions in experiment 3 (Table 8.5). The Port Meadow non-submerged site stolons would have been predicted to have a dry weight per mm greater than the other two sites, rather than less (Table 8.6).

However, in May the dry weight per unit length for stolons at the Port Meadow non-submerged site was more than double that at the other two sites (1.29 mg/mm; S.E.= 0.05; n= 10). Clearly, there was a dramatic fall in stolon dry weight per mm from May to June. The dry weight per unit length of petioles also fell from May to June (Table 8.3) and this, as already mentioned, mirrors the fall in mean total genet dry weight between the two months (Figure 8.2).

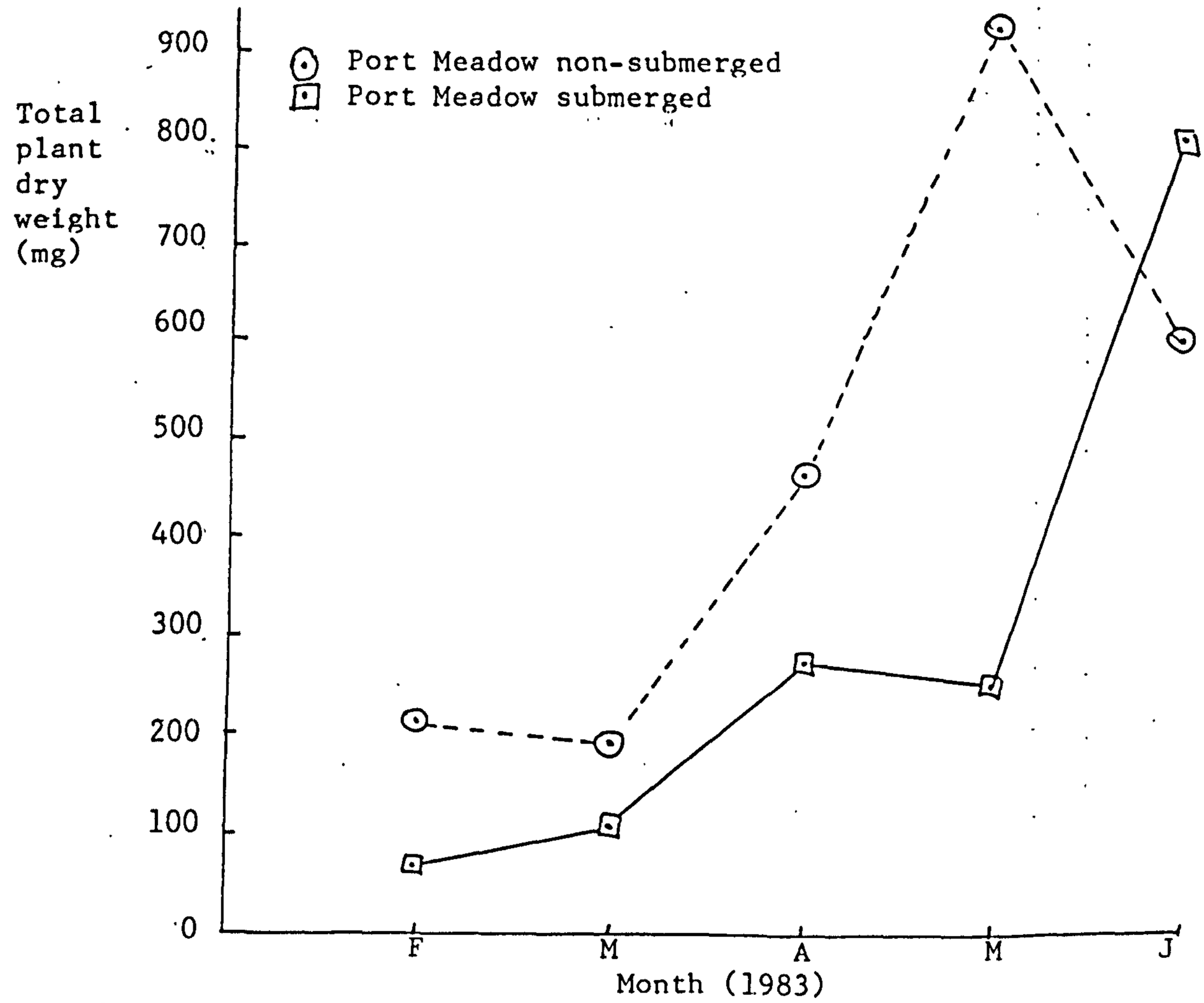


Figure 8.2

Total dry weights for R. repens plants collected from the two field sites from February to June 1983 (see Table 4.2).

8.3 Discussion

The results show that the dry weight per unit length of stolons and petioles can be reduced by submergence both in the short and long term. However, the overall picture for petioles appears to be less complex than that of stolons. For petioles a submergence treatment always resulted in a reduction in the dry weight per unit length (Tables 8.1 & 8.2). The results for petioles from experiment 3 suggest that the Port Meadow submerged site plants are genetically distinct from the other two populations based on dry weight per mm in the control treatment (Table 8.2). It is interesting to note that no genetic differentiation has been found between populations of R. repens, from sites with different submergence histories, with respect to the depth accommodation response in petioles (Ridge, per. comm.).

The field results for petioles (Table 8.3) can be explained in terms of the experimental results, the Port Meadow submerged site petioles showing lower dry weight per unit length than the other two sites under submergence.

From the experimental results the dry weight per unit length for stolons can be reduced by submergence (Tables 8.4 & 8.5). However, there is clear genetic differentiation with respect to stolon dry weight distribution between the populations studied (Table 8.5). This means that the origins of all experimental material must be taken into account when interpreting results. The plants in experiment 2 were from the Open University site (Table 8.4) and the results must be used with caution when discussing plants from the other sites. It is interesting that stolons from the Open University site did not show a reduction in dry weight per unit length after c. five months in Experiment 3 but did

in the shorter term experiment 2 (Tables 8.4 & 8.5).

Unlike the petioles the field results for stolon dry weight per unit length in June (Table 8.6) do not agree with experimental results (Table 8.5). This disagreement in results may be related to the large fall in dry weight per cm of stolon from May to June in the Port Meadow non-submerged site (Table 8.6). Petioles also show this fall from May to June in this site (Figure 8.1) and so does mean total dry weight per genet (Figure 8.2). This site suffered from drought during June and this may have caused the changes in dry weight per unit length and total genet dry weight.

Ginzo and Lovell (1973a; 1973b) suggest that reduction of dry weight per unit length of stolons in R. repens in response to decreased nitrogen supply was part of a strategy to compensate for the reduction in assimilate, the overall result is that total stolon length (and vegetative spread) are maintained with less dry weight investment. They also found that low nitrogen resulted in fewer, longer stolons. They suggest that this is another part of the strategy whereby ramets, borne on stolons, are placed as far as possible away from the parent in an unfavourable situation. Also, McIntyre (1965) found that the dry weight per unit lenth of Agropyron repens rhizomes decreased with decreasing nitrogen supply.

Can a similar strategy concerning stolons be seen in response to submergence stress? Stolons from the Port Meadow sites do show reduction in dry weight per unit length. There is evidence for the maintenance of stolon length from field and experimental results (Tables 8.7 & 8.8) in Port Meadow site plants. The Open University site plants do show short term changes in stolon dry weight per unit length

Table 8.7

The number of stolons, individual stolon length and total stolon length (mean and S.E.) for R. repens plants at harvest, grown in experiment 2.

Treatment	Stolons /plant	Individual stolon length (cm)	Total stolon length/plant (cm)	n
Controls	6.1 (0.8)a**	42.3 (9.3)a	257.7 (47.7)a	11
4-week submerged	2.2 (0.2)b	34.4 (7.4)a	74.6 (14.6)b	12
8-week submerged	1.5 (0.2)c	6.3 (1.5)b	9.5 (2.8)c	6

** different superscript means significantly different at $p<0.05$ (t-test).

Table 8.8

The number of stolons, total stolon length and individual stolon length (per plant, mean and and S.E.) for R. repens plant collected from the three field sites during June 1983 (n= 10).

Site	Number of stolons	Total stolon length (mm)	Length of individual stolons (mm)
Port Meadow submerged	1.6 (0.2)a	468 (48.7)a	292.6 (53.2)a
Port Meadow non-submerged	1.6 (0.3)a	405 (99.9)ab	253.1 (68.5)a
Open University	1.8 (0.2)a	273 (20.4)b	151.9 (22.3)b

and short term maintenance of stolon length (Table 8.7), however, because these are not true in the long term (Table 8.8) and considering the stolon internode length changes (Chapter 7) there is evidence that these plants show a different submergence strategy compared to the Port Meadow plants.

Do petioles show a similar length/number strategy to stolons in response to submergence? The results for petiole length and numbers from experiment 1 (Table 8.9) show that 13 week submerged rosettes sacrifice petiole number for individual petiole length. However, the 5 week submerged plants have maintained petiole number at the expense of individual petiole length.

Field results for the number of petioles per plant, total petiole length and individual petiole length (Table 8.10a-c) show that the Port Meadow submerged site plants have reduced petiole numbers and greater individual petiole length (Table 8.10a & c).

This strategy increases the probability of a few, long petioles reaching the water surface and the dramatic increase in dry weight gain that this achieves (see Chapter 3). The switch in the 5 week submerged rosettes to maintain petiole number is perhaps related to leaf area being a major determinant of photosynthetic capacity, rather than petiole length (this is important because of shading, hence the difference in petiole length in these plants is relatively small).

Overall many elements of the strategy for stoloniferous growth proposed by Ginzo and Lovell (1973a; 1973b) for nitrogen stress conditions can be seen in the response of R.repens stolons to submergence in the Port Meadow plants. A similar strategy can be proposed for petioles (with

Table 8.9

The number of petioles, total petiole length and individual petiole length (per plant, mean and S.E.) for R. repens plants grown in experiment 1.

Treatment	Number of petioles	Total petiole length (cm)	Length of individual petioles (cm)
Controls	8.6 (0.5)a	100.5 (6.0)a	11.7 (1.0)a (n= 12)
5-week submerged	8.2 (0.5)a	78.4 (6.0)b	9.6 (1.2)a (n= 12)
13-week submerged	2.2 (0.4)b	38.2 (12.7)c	17.4 (2.6)b (n= 11)

Table 8.10a

Number of petioles per rosette (mean and S.E.) for R. repens plants collected from the three field sites February to June 1983 (n= 10 to 20).

Site	Month				
	February	March	April	May	June
Port Meadow submerged	2.4 (0.2)^{b**}	4.7 (0.2)^{c}	5.7 (0.3)^{de}	5.0 (0.5)^{cd}	2.0 (0.4)^{ab}
Port Meadow non-submerged	5.1 (0.2)^{cd}	6.3 (0.4)^{ef}	8.9 (0.8)^{g}	7.4 (0.6)^{fg}	1.8 (0.4)^{ab}
Open University	12.5 (0.7)^{h}	9.1 (0.9)^{g}	n/a	n/a	1.1 (0.3)^{a}

** different superscript means significantly different at $p<0.05$ (t-test).
n/a = no data collected.

Table 8.10b

Total petiole length per rosette (mean and S.E., cm) for R. repens plants collected from the three field sites from February to June 1983 (n= 10 to 20).

Site	Month				
	February	March	April	May	June
Port Meadow submerged	13.2 (1.4)^{a}	24.1 (1.9)^{cd}	35.2 (2.0)^{e}	37.8 (4.1)^{e}	30.1 (5.2)^{e}
Port Meadow non-submerged	16.8 (1.5)^{b}	19.9 (1.7)^{bc}	28.8 (3.4)^{de}	37.2 (3.2)^{e}	19.0 (4.3)^{abc}
Open University	59.1 (6.9)^{f}	31.4 (4.5)^{e}	n/a	n/a	n/a

Table 8.10c

Length of individual petioles (mean and S.E., mm) for R. repens plants collected from the three field sites from February to June 1983 (n= 10 to 20).

Site	Month				
	February	March	April	May	June
Port Meadow submerged	54.8 (3.4)^{b}	52.4 (3.8)^{b}	61.7 (4.2)^{bc}	74.8 (9.4)^{c}	150.6 (13.0)^{d}
Port Meadow non-submerged	33.1 (2.0)^{a}	31.4 (2.4)^{a}	32.3 (2.5)^{a}	50.3 (3.5)^{b}	79.5 (12.6)^{c}
Open University	46.3 (4.7)^{b}	30.0 (3.0)^{a}	n/a	n/a	n/a

their leaves).

8.4 Summary

1. Petioles of R. repens plants show reductions in dry weight per mm of length with submergence independent of plant site of origin.

2. Stolons of R. repens plants can also show reductions in the dry weight per mm of length with submergence but this is dependent on site of origin.

3. These differences, along with differences in number and individual length of stolons, have been interpreted as part of a 'getting away' strategy.

Chapter 9

Leaf Demography and Submergence in Ranunculus repens

"..the assimilate fixed in leaves is not used solely to increase the number of leaves, but also to synthesize other structures.."

(Lovett Doust, 1981b)

9.1 Introduction

Initially, observations on Ranunculus repens rosettes when first submerged suggested that, apart from the increase in petiole length through the depth accommodation response (see section 1.8), there was a reduction in the number of leaves in the submerged rosettes compared to the controls (S.J. Smith pers. obs.). This reduction in the number of leaves in submerged rosettes has been interpreted as part of a strategy in which resources are concentrated into fewer younger leaves with longer petioles (see Chapter 8). This is somewhat similar to the strategy suggested for R. repens stolons in response to low nitrogen levels by Ginzo and Lovell (1973a;1973b).

The reduction in the number of leaves in submerged rosettes was thought to have resulted from an increase in the rate of mortality of the oldest leaves. To test this hypothesis the mortality rate of freshly submerged leaves needs to be studied in detail and so the demography of leaves was followed during the first few weeks of submergence. Stolon demography was also followed during the leaf demography study in order to determine

any influence of submergence on the number of stolons.

9.2 Experimental results

9.2.1 Leaf demography

The leaf demography of rosettes of R. repens was followed under three different treatments: air grown for 8 weeks (control), submerged for 4 weeks and then air grown for 4 weeks, and submerged for 8 weeks (full details under experiment 2 in section 2.4). Petioles were marked at weekly intervals with different coloured plastic straws.

Rosettes from all treatments show an initial (after the first week) fall in the number of leaves/rosette (Figure 9.1). Differences between treatments in the number of leaves/rosette started to show after four weeks when the number of leaves/rosette in the control treatment ceased to fall. In the following weeks the number of leaves/rosette in the control treatment rose at a nearly constant rate of about two leaves per week (Figure 9.1).

However, rosettes in the 4 week submergence treatment continued to show a reduction in the number of leaves/rosette until after the sixth week (Figure 9.1). In the seventh and eighth weeks the decline ceased and there was a tendency to increase. The 8 week submerged rosettes show a decrease in the number of leaves/rosette throughout the eight weeks (Figure 9.1).

The number of leaves/rosette is dependent on the "birth" rate (production of new leaves) and "death" rate of leaves. During the first

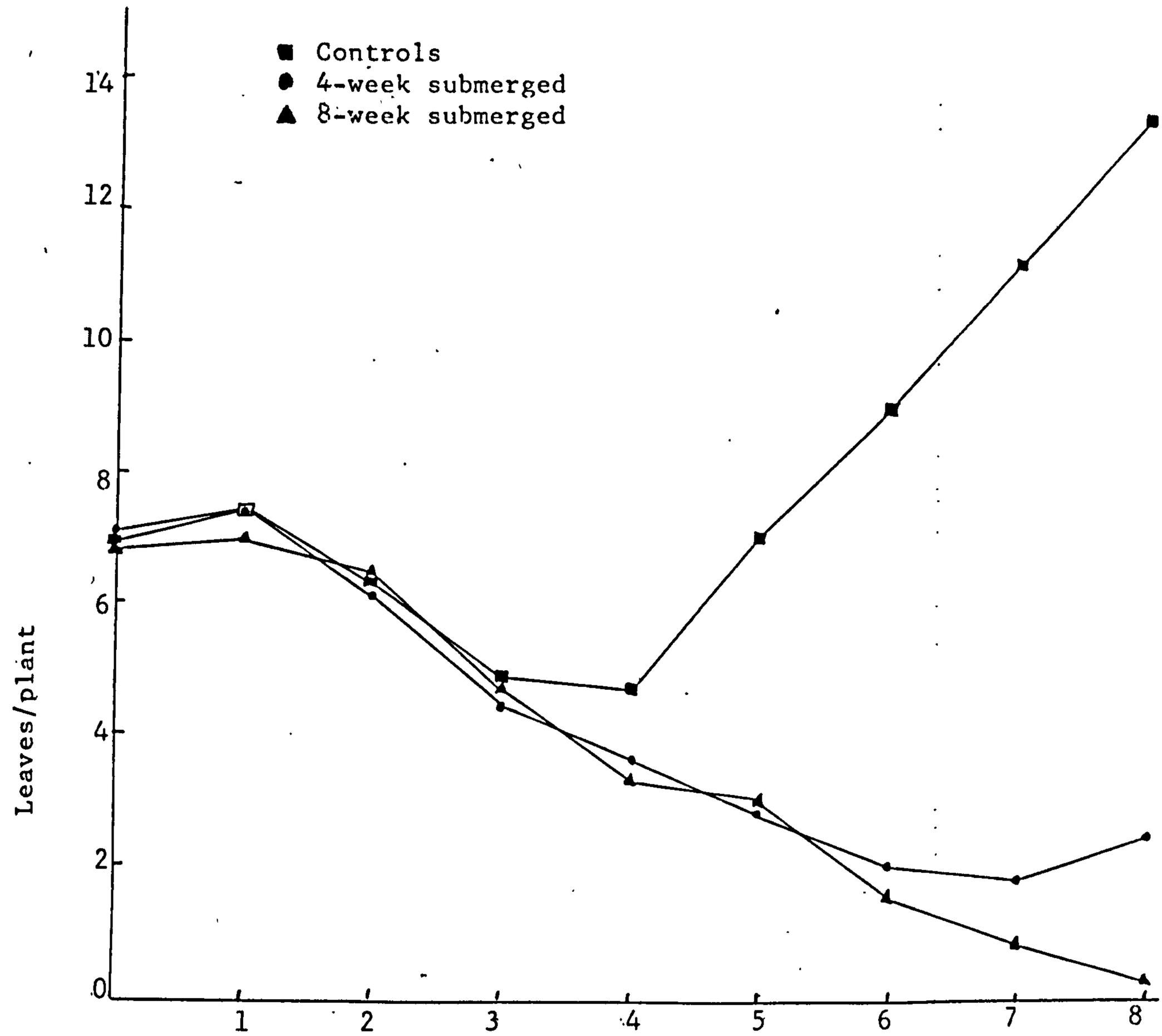


Figure 9.1

The number of leaves (mean per plant) for R. repens plants in experiment 2 (n= 12).

four weeks the birth rate of leaves is more than halved by submergence (Table 9.1). Transfer to air (in the 4 week submerged plants) doubled the birth rate of leaves during the second four weeks, to the level of the birth rate of the leaves in the control treatment during the first four weeks of the experiment (Table 9.1). However, during the same period (weeks five to eight) the control rosettes dramatically increased the rate of leaf production to nearly four times the initial rate (Table 9.1). The rate of production of new leaves in the 8 week submerged rosettes did not significantly change during weeks five to eight from the first four weeks (Table 9.1).

During the first four weeks leaf death rates were very similar for all treatments (Table 9.2). However, for weeks five to eight the control rosettes had much lower leaf death rates compared with the submergence treatment rosettes (Table 9.2). During the same period rosettes from both submergence treatments had very similar death rates even though the 4 week submerged rosettes spent the whole of this period in air (Table 9.2).

Leaf birth and death rates can be considered together by calculating 'leaf turnover'. This is leaf birth rate minus leaf death rate, and is expressed on a daily basis (see Lovett Doust, 1981b). Leaf turnover is a measure of the growth rate of the leaf population.

There is negative growth (i.e. a reduction) in the leaf population in all treatments for the first four weeks but the reduction is much greater in the submerged rosettes (Table 9.3). In weeks five to eight the leaf population in the control rosettes is increasing whereas in the submergence treatments the leaf populations are still decreasing but the reduction is greater in 8 week submerged rosettes compared to 4 week

Table 9.1

The number of leaves produced (per plant, mean and S.E.) by R. repens plants during weeks 1 to 4 and weeks 5 to 8 of experiment 2 (n= 12).

Treatment	weeks 1-4	weeks 5-8
Controls	2.5 (0.3)a**	9.9 (1.3)b
4-week submerged	1.0 (0.3)c	2.2 (0.4)a
8-week submerged	1.2 (0.3)c	0.5 (0.2)c

** as in all tables different superscript means significantly different at $p<0.5$ (t-test).

Table 9.2

Mortality of leaves (per plants, mean and S.E.) for R. repens plant during weeks 1 to 4 and 5 to 8 of experiment 2 (n= 12).

Treatment	weeks 1-4	weeks 5-8
Controls	4.8 (0.6)a	1.2 (0.2)b
4-week submerged	4.6 (0.3)a	3.3 (0.3)c
8-week submerged	4.7 (0.1)a	3.6 (0.4)c

Table 9.3

Turnover of leaves (mean daily rate/plant) in R. repens plants during weeks 1 to 4 and 5 to 8 of experiment 2 (n= 12).

Treatment	weeks 1-4	weeks 5-8
Controls	-0.082	+0.311
4-week submerged	-0.129	-0.039
8-week submerged	-0.125	-0.111

submerged rosettes (Table 9.3).

By separating leaves into age classes (or cohorts) leaf survival (or death) can be studied according to leaf age. The survivorship (strictly depletion; Harper, 1977) of leaves present at the start of the experiment (of mixed age and therefore not a cohort) shows no marked differences between the treatments until the sixth week of the experiment (Figure 9.2). However, during the following two weeks rosettes from both the submergence treatments lost all their initial leaves. The 8 week submerged rosettes lost all the initial leaves one week earlier than the 4 week submerged ones (Figure 9.2). The control rosettes still had about 18% of their initial leaves after eight weeks.

Differences between treatments in the survivorship of the first cohort of new leaves (produced during the first two weeks of the experiment) appeared in the sixth week (Figure 9.3). The 4 week submerged rosettes showed a delay in senescence compared to the 8 week submerged rosettes (Figure 9.3). However, in both submergence treatments all cohort 1 leaves died by week eight compared to twelve percent death of cohort 1 leaves in the control rosettes (Figure 9.3).

There was a delay of four weeks for differences between treatments to appear in the survival of the second cohort of new leaves (produced during weeks three and four) (Figure 9.4). Survival of these leaves in the 4 week submerged rosettes was very much better than those of the 8 week submerged rosettes, and almost as high as the control rosettes (Figure 9.4).

The third cohort of new leaves show differences between treatments two weeks later (in week eight) (Figure 9.5). Survivorship of these leaves

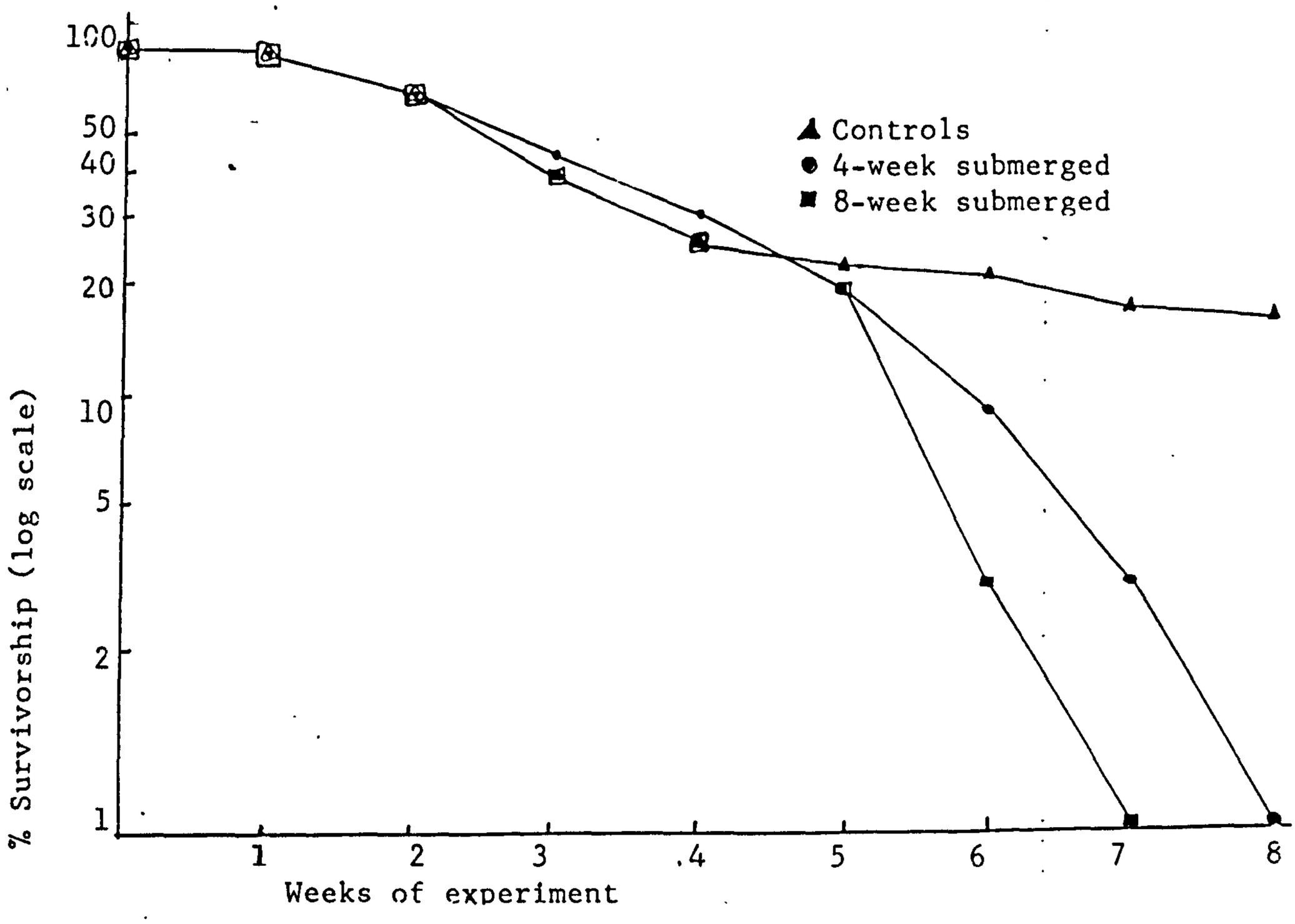


Figure 9.2

Depletion curves for the original leaves of the R. repens plants in experiment 2.

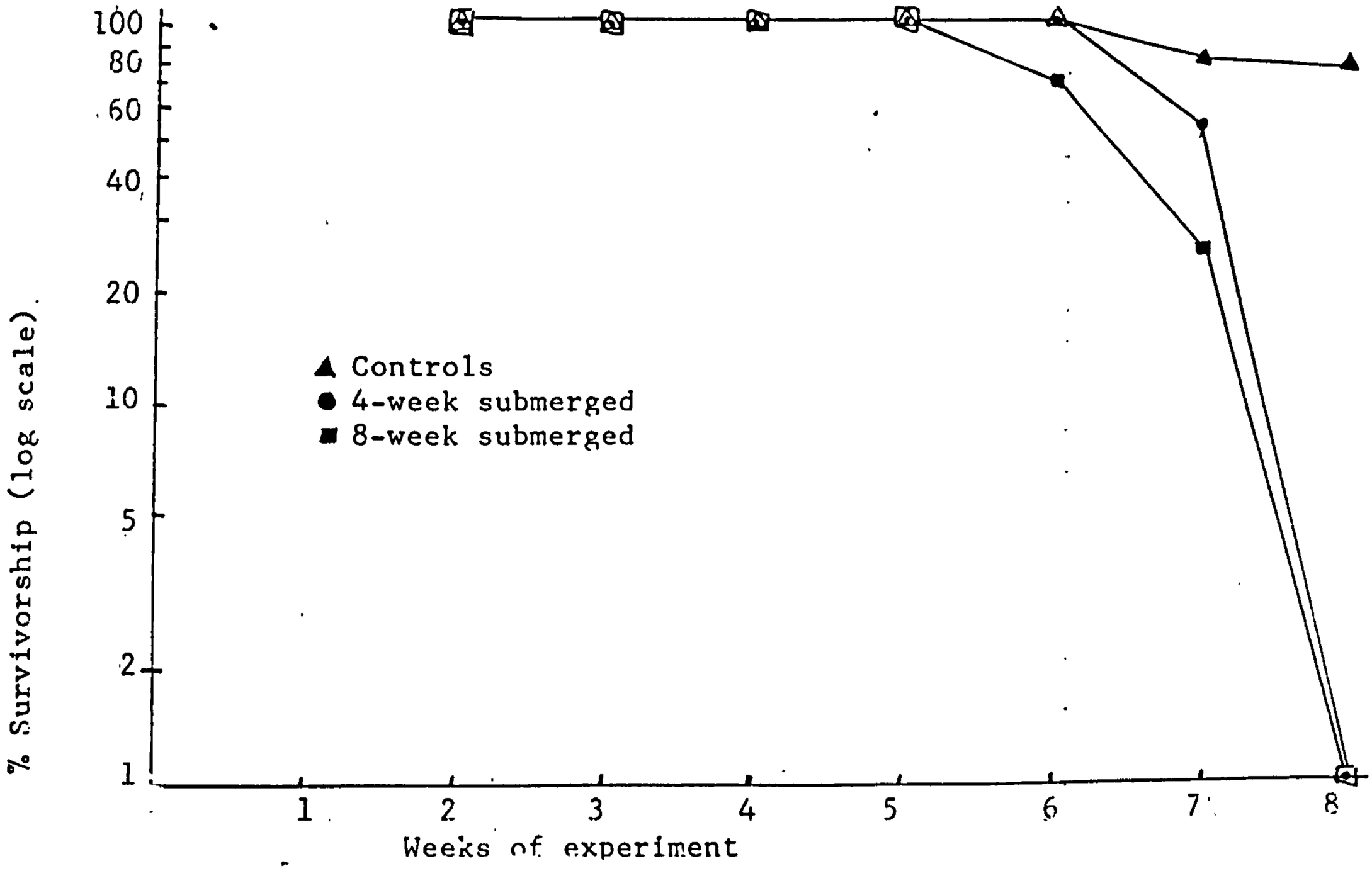


Figure 9.3

Survivorship curves for first cohorts of leaves in the R. repens plants in experiment 2.

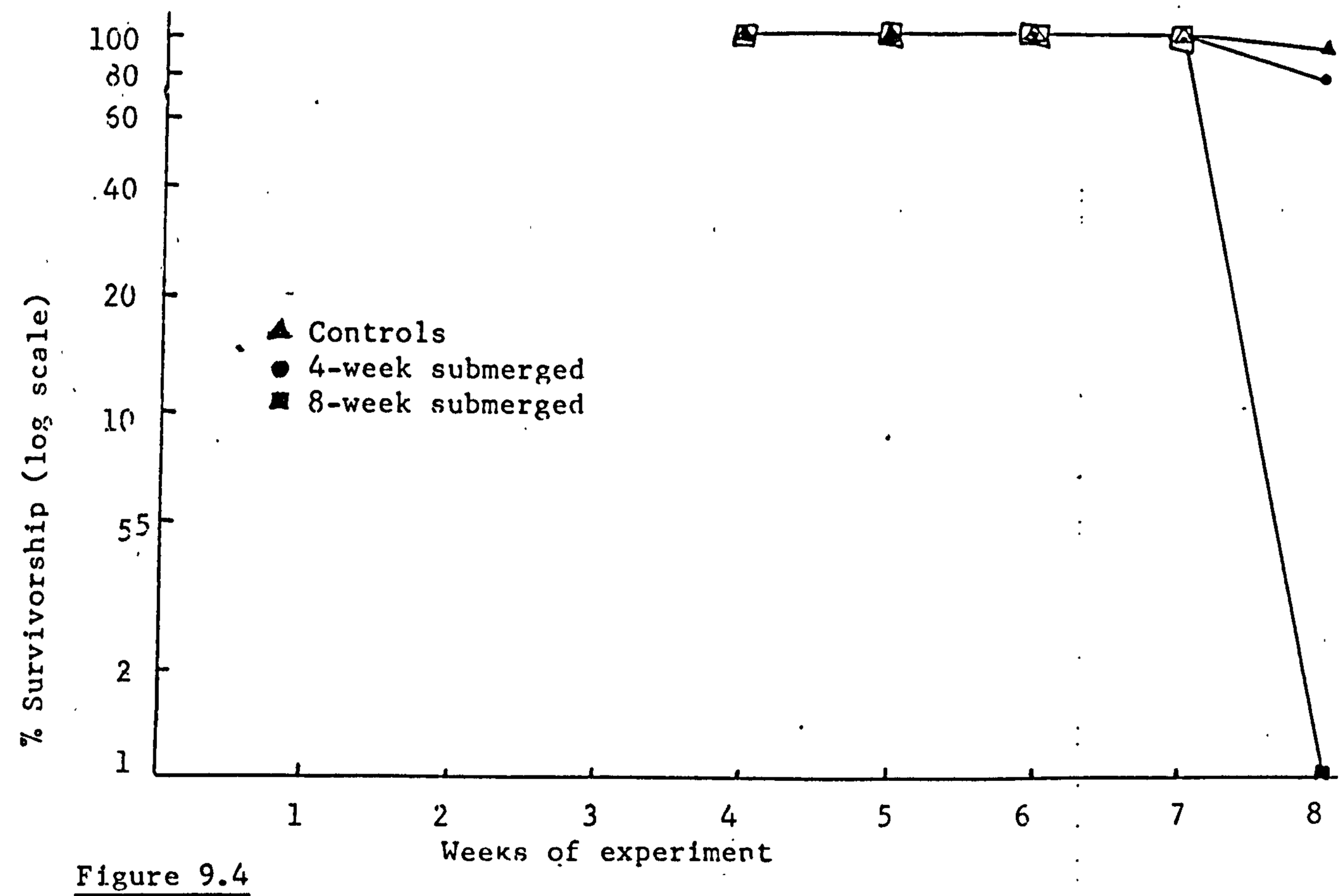


Figure 9.4

Survivorship curves for the second cohorts of leaves in the R. repens plants in experiment 2.

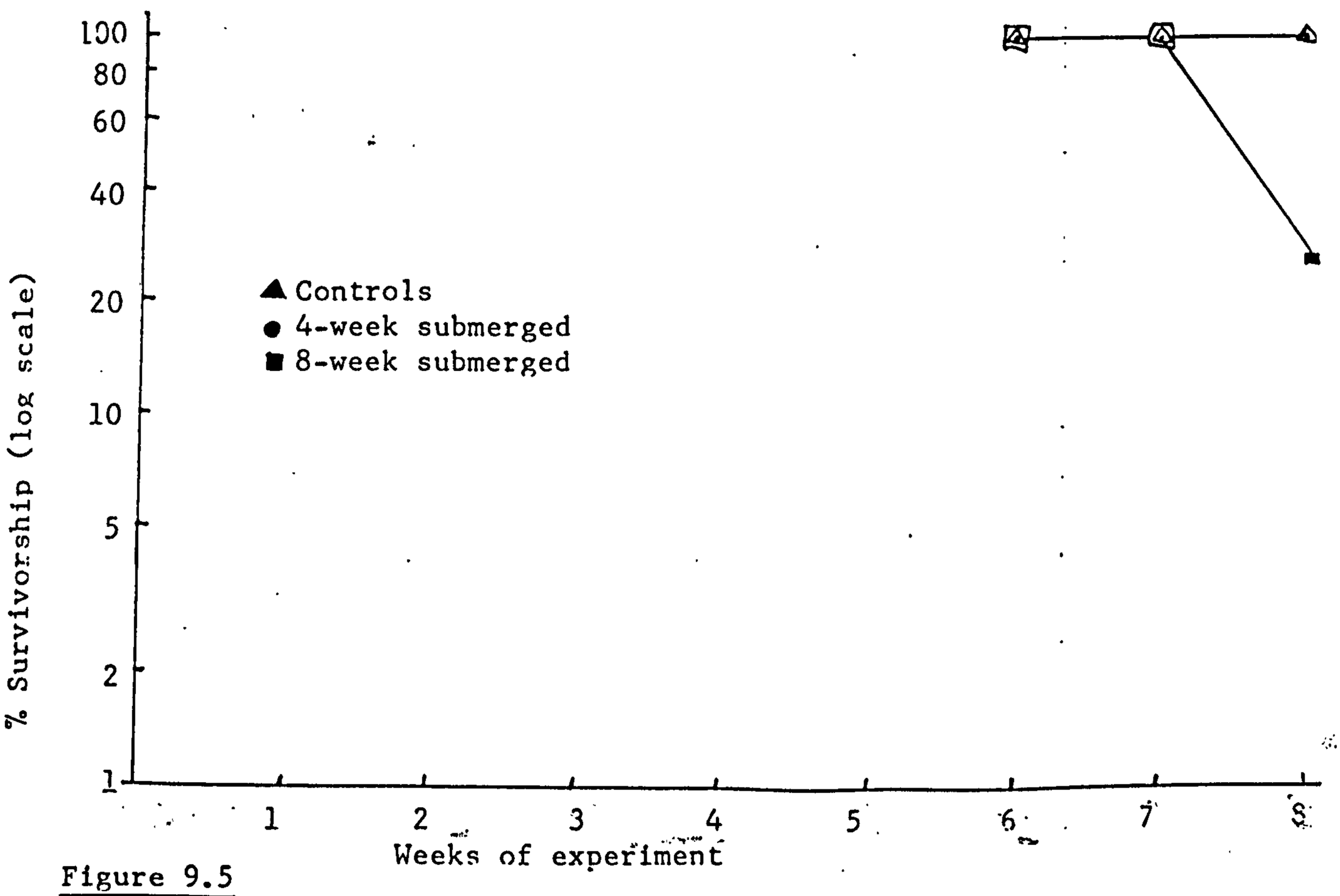


Figure 9.5

Survivorship curves for the third cohorts of leaves in the R. repens plants in experiment 2.

in the control and 4 week submergence treatment are very similar whereas the 8 week submergence treatment rosettes show rapid loss of these leaves.

9.2.2 Stolon Demography

The stolons produced during the leaf demography study were marked in the same way as leaves and their demography followed. There were no significant differences between treatments in the numbers of stolons produced during either the first four weeks or weeks five to eight (Table 9.4). Stolon death was minimal and this was restricted to the 8 week submerged rosettes and occurred only in week eight. One-fifth of the fifteen stolons produced by these rosettes died in that week. The number of stolons/rosette at harvest (four weeks after week eight) shows that there was much less production of new stolons during the four weeks before harvest in the submerged treatments (all growing in air during this period) compared to the control treatment rosettes (Table 9.5).

9.3 Discussion

Clearly submergence has an effect on the number of leaves/rosette, although differences did not appear until 4 weeks after submergence (Figure 9.1). This is in contrast to earlier observations which suggested differences within a week. The reason for this discrepancy is probably related to temperature. Earlier experiments were conducted in the greenhouse at around 20°C, whereas this experiment was conducted at ambient temperatures during March to May.

Table 9.4

The number of stolons (per plant, means and S.E.) produced by *R. repens* plants during weeks 1 to 4 and 5 to 8 of experiment 2 (n= 12).

Treatment	weeks 1-4	weeks 5-8
Controls	0.7 (0.1)[a]	0.2 (0.1)[b]
4-week submerged	0.9 (0.1)[a]	0.2 (0.1)[b]
8-week submerged	1.0 (0.1)[a]	0.3 (0.1)[b]

Table 9.5

The number of stolons per plant (mean and S.E.) of *R. repens* at week 12 of experiment 2 (at harvest).

Treatment	Stolons/plant	n
Controls	6.1 (0.8)[a]	11
4-week submerged	2.2 (0.2)[b]	12
8-week submerged	1.5 (0.2)[c]	6

Differences in the number of leaves/rosette between the control and submerged treatments in the first four weeks are due to differences in **leaf birth rate** (Table 9.1), whereas, during weeks five to eight differences in the number of leaves/rosette are due to both a decreased **death rate** and an increased **birth rate** in the controls (Tables 9.1 & 9.2). Differences in the number of leaves/rosette between the two submergence treatments were solely due to an increase in **leaf birth rate** in the 4 week submerged plants during their period in air (Tables 9.1 & 9.2).

Leaves of both cohorts 1 and 2 show a delay of about four weeks before submergence affects survival (Figures 9.3 & 9.4). The greater delay (six weeks) for submergence to affect survival in the initial leaves (Figure 9.2) shows that older leaves are either less affected, or take longer to be affected, by submergence than younger leaves. The leaves of cohort 3 are affected more rapidly (two weeks) than other leaves (Figure 9.5).

Can these findings be explained? Possibly the lack of resources after six weeks submergence results in the production of 'sub-standard' leaves that can not tolerate submergence, or perhaps the toxic products of anaerobic respiration (see section 1.8) build up with time and so have a greater effect. The latter hypothesis is supported by the fact that the rapid loss of cohort-3 leaves (in week eight) coincides with the loss of all older leaves (Figures 9.1, 9.2, 9.3, 9.4 & 9.5) in the 8 week submerged rosettes.

The greater survival of leaves following transfer to air after four weeks submergence is evident in all cohorts of leaves, and the initial leaves (Figures 9.2, 9.3, 9.4 & 9.5). There is also increased leaf

survival with increased time in air. This result is contrary to observations on submerged leaves of Ranunculus sceleratus which when exposed to air rapidly desiccate and die (see Chapter 11). This is possibly related to the greater commitment made by R. sceleratus petioles during submergence, e.g. R. sceleratus has a larger and faster depth accommodation response (Ridge, unpublished)

In contrast to leaf production, stolon production was not affected by submergence during the eight weeks of demographic study (Table 9.4). However, the number of stolons/rosette at harvest (four weeks later) (Table 9.5) shows that submergence does eventually affect the number of stolons/rosette. With this criterion the 4 week submerged rosettes show only a very slight 'recovery' from submergence (Table 9.5).

Turnover rates for the leaf populations (Table 9.3) are much lower for the time of year than quoted by Lovett Doust (1981b) for R. repens. She gives values of 0.20 to 0.60 for March and April. The turnover rate for weeks five to eight in the control rosettes is within the range but all other rates are much lower. Lovett Doust (1981b) gives negative values for leaf turnover from May to October and suggests that this is because assimilate is going elsewhere (roots, stolons, etc.). The negative leaf turnover shown by the control rosettes in this study may be related to a diversion of resources, e.g. to roots, possibly due to transplant shock.

From earlier observations made on submerged rosettes it was predicted that differences in the number of leaves/rosette were due to submergence increasing the death rate of older leaves. However, initial differences in leaf number are due to changes in the **birth rate of leaves** alone. Later, changes in birth and death rate are responsible for differences. Differences in leaf number between the two submergence treatments are

also based on changes in birth rate alone.

How do these findings relate to the ecology of this species? Firstly the loss of leaf production during (and after) submergence could be the result of tactical re-allocation of limited resources. This could be to existing leaves (or primordia) (Lovett Doust, 1981b), increasing the chance of the elongating petioles reaching the surface (see Chapter 7), or to roots to aid nutrient capture and avoidance of the toxic products of submergence (see section 1.8).

The lesser effects of submergence on stolon production point to the role of stolons in a strategy for the avoidance of unfavourable conditions (Ginzo and Lovell, 1973a; 1973b; Lovett Doust, 1981b; and see Chapters 7 & 8).

9.4 Summary

1. The observed decrease in the number of leaves/rosette in submerged plants was thought to be related to an increase in the mortality rate of the older leaves.

2. This demographic study showed that this was not the case. Initially, differences in leaf number were solely due to differences in leaf birth rate. Later, however, differences in both leaf birth and leaf death rates are involved.

3. The later during submergence that leaves were produced, the sooner they died (i.e. submergence increased mortality).

4. Transfer of submerged leaves to air increased their survivorship. This is opposite to observations on R. sceleratus leaves after transfer to air.

5. During the demographic study submergence did not influence stolon production and only at the end of the study was stolon death rate increased by submergence.

Chapter 10

Seedling Submergence in Ranunculus sceleratus

"..the only real strategists .. are evolutionary theorists.."

(Ghiselin, 1974:41)

10.1 Introduction

The annual Ranunculus sceleratus (Celery-leaved Buttercup) is found on wet, bare mud by the sides of ponds, lakes and rivers (see section 2.3). The majority of seedling germination occurs in the autumn and spring (see Chapter 12). The over-wintering, autumn germinated seedlings are likely to be submerged in autumn, winter and spring, while the spring germinated seedlings are susceptible to spring submergence (see Chapter 12).

The influence of submergence of seedlings on the ecology of this species was studied. In this chapter the following questions were asked:

1. Does submergence as seedlings affect the adult plant? In particular do changes in dry weight allocation, especially to reproductive structures, occur?

2. Can an overall strategy for tactical allocation changes and differences in response to submergence be put forward?

Another dimension was added to this work by looking at the influence of nutrient level and its interaction with submergence. This is relevant to this species because of its association with nutrient rich conditions (Toorn, 1980; Fitter, 1978; Salisbury, 1970).

10.2 Experimental Results

This experiment involved seedlings of R. sceleratus being grown with or without a one week submergence treatment and in one of three John Innes composts (see experiment 4 section 2.4).

10.2.1 Phenology

Elongation of the flowering stem, flowering and seed production were not affected by nutrient level in either submergence or control treatments but these were all delayed in the submergence treatment plants by between 11 and 16 days (Table 10.1). The delay between the submerged and control plants appears to be shortening with time.

10.2.2 Dry Weights

Total dry weights (Table 10.2) were not significantly affected by the submergence treatment but there was a highly significant effect of John Innes "level". The John Innes No. 3 (JI3) plants have significantly greater total dry weights than the JI1 and JI2 plants. In the submergence treatment there is a significant reduction in total dry weight from JI1 to JI2 (Table 10.2).

Table 10.1

The timing of flowering stem elongation, flowering and seed production (mean and S.E.) in *R. sceleratus* plants of experiment 4 (n= 15).

	Treatment	
	Controls	Submerged
Days$^{\mu}$ to flowering stem elongation	38.5 (1.2)^{a}**	54.9 (1.3)^{b}
Days to flowering	50.2 (0.9)^{a}	63.8 (0.7)^{b}
Days to ripe seed production	66.7 (0.9)^{a}	78.3 (0.9)^{b}

μ days from seedling transplantation (2/2/83)
** as in all tables different superscript means significantly different at $p<0.05$ (t-test).

Table 10.2

Total dry weights (g, mean per plant) for *R. sceleratus* plants in experiment 4 (n= 5).

Treatment	John Innes number		
	1	2	3
Control	5.87^{b}**	5.37^{ab}	7.48^{c}
Submergence	6.07^{b}	4.83^{a}	7.35^{c}

Pooled S.E. = 0.26
Anova: Treatment n.s.; John Innes no. $p<0.001$; Interaction n.s.
** different superscript means significantly different at $p<0.05$ using pooled S.E. in t-test (see Mead and Curnow, 1983).

With the exception of the dry weight of receptacles all individual organs showed a significant submergence treatment effect (Table 10.3). However, overall submergence resulted in an increase in the dry weight of roots and leaves but a decrease in the dry weight of flowering stem and seeds (Table 10.3). John Innes level had a significant effect on all organs, involving an overall increase in dry weight from JI1 to JI3.

In general, organ dry weights either remained unchanged, or fell from JI1 to JI2 and then increased in the JI3 plants to a level above that of JI1 plants. An exception to this pattern was the dry weight of the flowering stem which showed no significant change with JI level in the control treatment (Table 10.3). The JI3 control and submerged plants show no effect of submergence with organ dry weights whereas an effect is often present in JI1 and JI2 plants (Table 10.3). With the dry weight of seeds the submergence effect is only seen in the JI1 plants. A significant interaction between submergence and JI level was found with the dry weights of flowering stems and roots.

10.2.3 Dry Weight Allocation

Dry weight allocation was analysed using percentages and not the graphical technique used elsewhere (see section 2.6). This was because the spread in total dry weights was too small to allow for an accurate assessment of allocation 'slopes'.

All organs showed a significant submergence effect on the allocation of dry weight (Table 10.4). The pattern of response was similar to the dry weights, with leaves and roots showing increased allocation with submergence and flowering stem, receptacles and seeds showing reduced

Table 10.3

Organ dry weights (g, mean per plant) for R. sceleratus plants in experiment 4 (n= 5).

(a) Roots

Treatment	John Innes number 1	2	3
Control	0.78^{b**}	0.43^{a}	1.42^{d}
Submergence	1.35^{d}	0.68^{b}	1.29^{d}

Pooled S.E. = 0.062
Anova: Treatment p<0.001; John Innes no. p<0.001; Interaction p<0.001.
** different superscript means significantly different at p<0.05 using pooled S.E. in t-test (see Mead and Curnow. 1983).

(b) Leaves

Treatment	John Innes number 1	2	3
Control	0.69^{ab**}	0.65^{a}	1.16^{c}
Submergence	0.90^{b}	0.85b^{a}	1.20^{c}

Pooled S.E. = 0.069
Anova: Treatment p<0.001; John Innes no. p<0.001; Interaction n.s.

(c) Flowering stem

Treatment	John Innes number 1	2	3
Control	2.59c**	2.56c	2.73^{c}
Submergence	2.19^{b}	1.77a	2.76^{c}

Pooled S.E. = 0.082
Anova: Treatment p<0.001; John Innes no. p<0.001; Interaction p<0.001.

Table 10.3 continued

(d) Receptacles

Treatment	John Innes number		
	1	2	3
Control	0.650^{b**}	0.592^{ab}	0.678^{b}
Submergence	0.634^{b}	0.512^{a}	0.654^{b}

Pooled S.E. = 0.036
Anova: Treatment n.s.; John Innes no. $p<0.025$; Interaction n.s.

(e) Seeds

Treatment	John Innes number		
	1	2	3
Control	1.16^{b**}	1.14^{ab}	1.49^{c}
Submergence	1.00^{a}	1.03^{ab}	1.45^{c}

Pooled S.E. = 0.046
Anova: Treatment $p<0.01$; John Innes no. $p<0.001$; Interaction n.s.

Table 10.4

Percentage dry weight allocation to organs (mean per plant) for R. sceleratus plants in experiment 4 (n= 5).

(a) Roots

Treatment	John Innes number 1	2	3
Control	13.3b**	7.9a	19.0c
Submergence	22.2a	13.9b	19.5c

Pooled S.E. = 0.52
Anova: Treatment p<0.001; John Innes no. p<0.001; Interaction p<0.001.
** different superscript means significantly different at p<0.05 using pooled S.E. in t-test (see Mead and Curnow, 1983).

(b) Leaves

Treatment	John Innes number 1	2	3
Control	11.7a**	11.9a	15.5b
Submergence	14.7b	17.4c	16.3bc

Pooled S.E. = 0.65
Anova: Treatment p<0.001; John Innes no. p<0.01; Interaction p<0.01.

(c) Flowering stem

Treatment	John Innes number 1	2	3
Control	44.3b**	47.9c	36.5a
Submergence	36.2a	36.7a	37.6a

Pooled S.E. = 0.83
Anova: Treatment p<0.001; John Innes no. p<0.001; Interaction p<0.001.

Table 10.4 continued

(d) Receptacles

Treatment	John Innes number 1	2	3
Control	11.0b**	11.0b	9.1a
Submergence	10.4b	10.5b	8.9a

Pooled S.E. = 0.25
Anova: Treatment $p<0.05$; John Innes no. $p<0.01$; Interaction n.s.

(e) Seeds

Treatment	John Innes number 1	2	3
Control	19.7b**	21.3c	20.0bc
Submergence	16.6a	21.4c	19.7b

Pooled S.E. = 0.51
Anova: Treatment $p<0.025$; John Innes no. $p<0.001$; Interaction $p<0.01$.

allocation (Table 10.4).

JI level also had a significant effect on allocation in all organs. Unlike the dry weight results, increased JI level reduced allocation to flowering stems and receptacles and increased allocation to seeds, leaves and roots (Table 10.4). With the exception of allocation to receptacles, allocation to all organs showed an interaction between submergence and JI level (Table 10.4). The JI3 plants again show the lack of a submergence effect often found in JI1 and 2 plants (Table 10.4).

10.2.4 Floral Structure

Submergence had a significant affect on several floral characters, including the number of seed heads/plant, the number of seeds/plant, the number of seeds/seed head and the dry weight/cm of flowering stem height (Table 10.5). Mean seed weight and flowering stem height were not significantly affected by submergence (Table 10.5). Of the characters affected by submergence only the number of seeds/seed head showed an increase with submergence.

JI level affected all characters except mean seed weight and only the height of the flowering stem showed a reduction from JI1 to JI3 (Table 10.5). The JI1 and JI2 plants are usually not significantly different within either control or submergence treatments, the exception being dry weight/cm of flowering stem height which also has the only significant interaction term between submergence and JI level within the floral characters (Table 10.5).

Table 10.5

Floral characteristics (mean per plant) for *R. sceleratus* plants in experiment 4 (n= 5).

(a) Height of flowering stem (cm)

Treatment	John Innes number 1	2	3
Control	60.2^{b**}	59.6^{b}	56.0^{a}
Submergence	61.0^{b}	58.8^{b}	58.8^{b}

Pooled S.E. = 0.69
Anova: Treatment n.s.; John Innes no. $p<0.001$; Interaction n.s.
** different superscript means significantly different at $p<0.05$ using pooled S.E. in t-test (see Mead and Curnow, 1983).

(b) Mean seed weight (mg)

Treatment	John Innes number 1	2	3
Control	0.23^{a**}	0.22^{a}	0.23^{a}
Submergence	0.23^{a}	0.23^{a}	0.23^{a}

Pooled S.E. = 0.003
Anova: Treatment n.s.; John Innes no. n.s.; Interaction n.s.

(c) Seeds/plant

Treatment	John Innes number 1	2	3
Control	5070^{bc**}	5270^{c}	6600^{d}
Submergence	4430^{a}	4530^{ab}	6210^{d}

Pooled S.E. = 195
Anova: Treatment $p<0.01$; John Innes no. $p<0.001$; Interaction n.s.

Table 10.5 continued

(d) Seed heads/plant

Treatment	John Innes number 1	2	3
Control	190.6b**	195.2b	242.2c
Submergence	150.0a	143.6a	183.4b

Pooled S.E. = 5.72
Anova: Treatment p<0.001; John Innes no. p<0.001; Interaction n.s.

(e) Seeds/seed head

Treatment	John Innes number 1	2	3
Control	26.5a**	27.0a	27.3ab
Submergence	29.6bc	31.9cd	34.0d

Pooled S.E. = 0.84
Anova: Treatment p<0.001; John Innes no. p<0.05; Interaction n.s.

(f) Dry weight per cm of flowering stem height (mg/cm)

Treatment	John Innes number 1	2	3
Control	43.0c**	43.0c	48.6d
Submergence	35.9b	30.0a	47.0d

Pooled S.E. = 0.98
Anova: Treatment p<0.001; John Innes no. p<0.001; Interaction p<0.001

Unlike dry weight and dry weight allocation submergence has significant effects on the JI3 plants. These effects were on the number of seed heads/plant, the number of seeds/seed head and flowering stem height (Table 10.5).

10.3 Discussion

10.3.1 Phenology

The delay in flowering in the submerged plants (Table 10.1) could have been a size effect; the rosettes of the submerged plants appeared smaller throughout the experiment. The lack of a submergence effect on total dry weight at harvest (Table 10.2) could in some part be due to the later harvesting of these plants but also to the fact that the differences between the submerged and control plants lessen with time (Table 10.1). This can be seen in the shortening of the time delay shown by submerged plants between stem elongation and seed production (Table 10.1).

Many monocarpic perennial plants have been shown to possess size-dependent flowering (Werner, 1975; Baskin and Baskin, 1979; Reinartz, 1984a). Salisbury (1970) suggests that R. sceleratus can behave as a monocarpic perennial under some conditions. However, Samarakoon and Horton (1981) found R. sceleratus (in Canada) to be a Long Day plant. It may be that size-dependent and Long Day control of flowering are found in this plant (see Chapter 12).

Whether or not the 10 day delay in seed production is ecologically meaningful is debatable. If conditions are such that seeds enter the

seed bank at the time of seed fall then it is probably not. If however, seed germination takes place at seed fall, then the early germinating seeds could have an advantage over the later germinating ones (Cook, 1980; see also Chapter 12).

10.3.2 Dry weights and dry weight allocation

The lack of a submergence effect on total dry weight hides considerable effects of submergence on the component organs (Tables 10.2 & 10.3). The submergence treatment affected most dry weights (except receptacle) and all dry weight allocations. The response of the various organs to the submergence treatment was different for reproductive (seeds, flowering stem and receptacles) and non-reproductive organs (leaves and roots). The reproductive organs showed decreased, or no change in, dry weight and allocation whereas non-reproductive organs showed an overall increase with submergence (Tables 10.3 & 10.4).

With the exception of allocation to flowering stem and receptacles, all other allocations (and all organ dry weights) increased from JI1 to JJ3 (Tables 10.3 & 10.4). The response of "reproductive allocation" in annuals to reduced nutrients has been studied and some general conclusions can be drawn.

There are, however, two problems with a review of these results. Firstly, a terminological one, since what is regarded as "reproductive allocation" varies from author to author (see section 2.1) and secondly, the nutrient levels and plant species used varied between studies. Generally, authors used the term "reproductive allocation" in two ways. There are those who use it to refer to only seed allocation and those

who include allocation to other reproductive structures (henceforth "floral" allocation).

Lowering nutrient levels often results in no change in "reproductive allocation" (both seed and floral allocation) (see Andel and Vera, 1977; Harper and Ogden, 1970; Raynal and Bazzaz, 1975; Steen, 1984; Waite and Hutchings, 1982). Only one study (Snell and Burch, 1975) has found a decrease in "floral" allocation with a lowering of nutrient level.

Other stresses have different effects on reproductive allocation. Increased density results in decreased percentage "floral" allocation (Hiroi and Monsi, 1966; Pemadasa, 1976; Snell and Burch, 1975; Waite and Hutchings, 1982) and no change in seed allocation (Raynal and Bazzaz, 1975; Waite and Hutchings, 1982).

Other stresses have been little studied but drought stress resulted in no change in seed or floral allocation (Abrahamson and Hershey, 1977). However, Hickman (1975) found that seed allocation in Polygonum cascadense increased along a gradient of a '..broad range of physical stresses..' (mainly increasing drought and density stress). Hiroi and Monsi (1966) found that floral allocation in sunflower plants increased with low light intensity at high densities but showed no change under the same conditions at low density.

An explanation for the decreased reproductive allocation with increased density has been put forward by Hickman (1975). He suggests that the additional vegetative allocation increases the competitive ability of the individual. Also Fitter and Hay (1981) review evidence that drought, nutrient, low temperature and oxygen stress generally result in increased root allocation.

The reduction in seed allocation with submergence agrees with many of the reports mentioned above for other stresses. An explanation similar to the Hickman (1975) explanation for the same result with density stress could be put forward.

The submerged plants were much smaller in the early stages of the experiment (S.J.Smith pers. obser.) and so an increased allocation to root and leaves would result in a greater resource capture. This may also explain the delay in flowering that was synonymous with a delay in leaf senescence which occurs rapidly after the first seeds ripen. This has been observed in the field as well as in the greenhouse (S.J.Smith pers. obser.). Increasing resource capture with time may also explain the decreasing delay between submerged and control plants from flowering stem elongation to seed production.

Another part of this strategy may be the change in dry weight/cm of flowering stem height. This results in the maintenance of flowering stem height with less resources. Although flowering stem height over a large range (5cm to 55cm) has been shown to be related to seed output (see chapter 12), the range of heights in this experiment (55cm to 63cm) does not reflect this. This is probably due to the small range of heights in question. At these heights the number of seeds/plant is affected only slightly by changes in height (see Chapter 12). Height maintenance may be related to dispersion of seeds rather than seed number (Harper, 1977).

The JI3 plants showed no significant submergence effects with dry weight allocation, however, the control JI3 plants are significantly different from the submerged ones with respect to several floral characteristics.

10.3.3 Floral structure

The reduction in the seed heads/plant (Table 10.5) can to some extent be attributed to the change in the structure of the flowering stem. This has already been mentioned regarding the distinction between rosette and flowering stem leaves (see section 2.4). The flowering stems of the submerged plants were less branched, with fewer side branches and these were also less branched. As flowers are mainly borne at the ends of branches this resulted in fewer sites for flowers and hence seed heads.

The reduction in seeds/plant (Table 10.5) was not as great as the reduction in the seed heads/plant because submerged plants showed an increase in the number of seeds/seed head. This can be explained as a means of maintaining, as far as possible, the seed output of this annual plant when flowering sites are reduced.

However, mean seed weight was unaffected by submergence (Table 10.5). R. sceleratus has shown a relatively large range of possible mean seed weights (0.08mg to 0.25mg have been recorded: Smith, unpublished; Grime, 1979; Grime et al, 1981; Salisbury, 1942; 1970). Mean seed weight is one of the least plastic of plant characteristics (Harper, 1977) and several studies have shown mean seed weight to be closely related to the ecology of a species (Salisbury, 1942; 1974; Baker, 1972; Silvertown, 1981). The results here suggest that although this species has variable mean seed weight this character generally does not vary within plants grown under similar conditions.

10.4 Why do JI3 plants show a limited response to submergence?

Plants grown on the highest nutrient treatment (JI3) showed no differences in organ dry weights or dry weight allocation with submergence-but they did show differences in several floral characteristics. The loss of a submergence effect on dry weight allocations at high nutrient levels may explain the association of this species with fertile soils (Salisbury, 1970; Toorn, 1980; Fitter, 1978).

What are the reasons for this lack of a submergence effect? Three answers to this question are possible:

1. Higher nutrient levels during the submergence treatment prevented, or compensated for, any allocation differences that occurred at lower nutrient levels.

2. Higher nutrient levels after the submergence treatment enabled plants to compensate for allocation differences during submergence.

3. A combination of both the above.

To answer this question the above experiment was repeated but this time it was stopped immediately after the submergence treatment in order to assess the effects of submergence and its possible interaction with JI level.

10.5 Dry weight allocation of seedlings following submergence

10.5.1 Experimental results

This experiment involved the harvesting of seedlings that had been grown under control or a one week submergence treatment at three nutrient levels (see section 2.4 under experiment 5).

Hypocotyl lengths did not change from their time-zero values and there were no obvious macro-structural changes (Table 10.6). Submergence did not affect the length of cotyledon-petioles but there was a significant increase in length from the time-zero controls (Table 10.6). Nutrient level had no significant effects on cotyledon-petioles and hypocotyl lengths (Table 10.6).

The petioles of the first true-leaves were not significantly different in length (Table 10.6) but those of the submerged seedlings appeared much thinner in diameter and were not as rigid as those of the control seedlings. This was also true of the petioles of the second true-leaves.

The petioles of the second true-leaves in the submerged seedlings were significantly longer than those of the control seedlings (Table 10.6). The submerged seedlings, however, lacked the third true-leaves and their petioles found in all the control seedlings (Table 10.6).

Total leaf area was much smaller in the submerged seedlings compared with control seedlings, although it had increased from time-zero (Table 10.7). Again nutrient level had no significant effect.

Table 10.6

Lengths of hypocotyls, cotyledon petioles and petioles of the first, second and third true leaves (mm, per plant mean and S.E.) for *R. sceleratus* plants in experiment 5 (n= 5).

(a) Hypocotyl lengths

Treatment	John Innes number 1	2	3
Time-zero control	12 (0.9)a**	12 (0.5)a	12 (0.5)a
Submergence	12 (0.5)a	12 (0.5)a	12 (0.5)a
Control	11 (0.9)a	11 (0.9)a	11 (0.9)a

** different superscript means significantly different at $p<0.05$ (t-test).

(b) Lengths of cotyledon petioles

Treatment	John Innes number 1	2	3
Time-zero control	2 (0.5)b**	2 (0.5)b	2 (0.5)b
Submergence	5 (0.5)a	4 (0.5)a	4 (0.5)a
Control	5 (0.5)a	5 (0.5)a	5 (0.5)a

(c) Lengths of petioles of first true leaves

Treatment	John Innes number 1	2	3
Time-zero control	2 (0.5)b**	2 (0.5)b	2 (0.5)b
Submergence	16 (1.4)a	16 (1.8)a	17 (0.9)a
Control	17 (1.4)a	17 (2.3)a	17 (1.4)a

Table 10.6 continued

(d) Lengths of petioles of second true leaves

Treatment	John Innes number 1	2	3
Time-zero control	0a**	0a	0a
Submergence	53 (4.5)b	53 (4.5)b	54 (5.0)b
Control	18 (0.9)c	19 (3.2)c	19 (1.4)c

(e) Lengths of petioles of third true leaves

Treatment	John Innes number 1	2	3
Time-zero control	0a**	0a	0a
Submergence	0a	0a	0a
Control	6 (1.8)b	7 (3.2)b	8 (1.8)b

Table 10.7

Leaf areas (both surfaces) for *R. sceleratus* plants (mm^2, mean and S.E. per plant) in experiment 5 (n= 5).

Treatment	John Innes number 1	2	3
Time-zero control	94 (4)a**	92 (10)a	90 (7)a
Submergence	119 (14)b	123 (4)b	126 (8)b
Control	203 (18)c	208 (35)c	199 (22)c

** different superscript means significantly different at $p<0.05$ (t-test)

Table 10.8

Total dry weights (mg, mean and S.E. per plant) for *R. sceleratus* plants experiment 5 (n= 5).

Treatment	John Innes number 1	2	3
Time-zero control	0.86 (0.10)a**	0.85 (0.13)a	0.80 (0.10)a
Submergence	1.55bA*	1.79bA	1.88bA
Control	5.70bB	6.42bB	6.68bB

Pooled S.E. = 0.68 (excluding time-zero controls)
Anova: treatment $p<0.001$; John Innes n.s.; Interaction n.s. (ex. time-zero controls).
** different lower case superscript means significantly different at $p<0.05$ (t-test) from the time-zero controls alone.
* different upper case superscript means significantly different at $p<0.05$ using pooled S.E. in t-test (see Mead and Curnow, 1983) (ex. time-zero controls).

The submerged seedlings had lower total dry weights than the control seedlings, and were between 1/3 and 1/4 of the dry weight of control seedlings and roughly twice the time-zero dry weights (Table 10.8). Nutrient level had no significant effect on total dry weights in the time-zero, control and submerged seedlings.

Relative growth rates (RGRs) (see Larcher, 1980:135) based on the mean total dry weights (Table 10.9) show that the control seedlings grew on average between 2.3 and 3.2 times faster than submerged seedlings (Table 10.9).

Leaf area differences can be taken into account using the net assimilation rates (NARs) (see Larcher, 1980:134). The NAR results show an even greater difference between control and submerged seedlings, with control NARs being on average between 4.1 and 5.1 times greater than those for the submerged seedlings (Table 10.10).

The dry weights of roots, petioles and leaves are all reduced by submergence but the reduction is not uniform (Table 10.11). Leaf dry weights on average show about a 2/3 reduction in dry weight (Table 10.11). Petiole dry weights show a lower reduction of between 1/2 and 2/3 (Table 10.11). Root weights show the greatest reduction being between 5/6 and 13/14 (Table 10.11).

Root dry weights show little increase from the time-zero values; the JI2 grown submerged plants show no significant differences in root dry weight (Table 10.11). Root weights show a significant nutrient level-submergence interaction. JI1 root weights are significantly lower than the JI3 plants in control treatment.

Table 10.9

Relative growth rates (mg/mg/day, mean per plant) for R. sceleratus plants in experiment 5 (n= 5).

Treatment	John Innes number 1	2	3
Submergence (S)	0.59	0.75	0.85
Control (C)	1.89	2.02	2.12
C/S	3.2	2.5	2.3

Table 10.10

Net assimilation rates (mg (dry weight)/mm²(leaf area)/week, mean per plant) for R. sceleratus plants in experiment 5 (n= 5).

Treatment	John Innes number 1	2	3
Submergence (S)	0.89	1.20	1.37
Control (C)	4.54	5.19	5.68
C/S	5.1	4.3	4.1

Table 10.11

Organ dry weights (mg, mean and S.E. per plant) for R. sceleratus plants in experiment 5 (n= 5).

(a) Leaves and cotyledons

Treatment	John Innes number 1	2	3
Time-zero control	52 (9)a**	49 (10)a	48 (7)a
Submergence	90bA*	109bA	113bA
Control	336bB	347bB	337bB

Pooled S.E. = 34.7 (excluding time-zero controls).
Anova: treatment $p<0.001$; John Innes n.s.; Interaction n.s. (ex. time-zero controls).
** different lower case superscript means significantly different at $p<0.05$ (t-test) from the time-zero controls alone.
* different upper case superscript means significantly different at $p<0.05$ using pooled S.E. in t-test (see Mead and Curnow, 1983) (ex. time-zero controls).

(b) Petioles and hypocotyl

Treatment	John Innes number 1	2	3
Time-zero control	23 (2)a**	24 (6)a	22 (4)a
Submergence	47bA*	56bA	59bA
Control	128bB	144bB	126bB

Pooled S.E. = 17.3 (excluding time-zero controls).
Anova: treatment $p<0.001$; John Innes n.s.; Interaction n.s. (ex. time-zero controls).

(c) Roots

Treatment	John Innes number 1	2	3
Time-zero control	11 (2)a**	12 (2)a	10 (1)a
Submergence	18aA*	13aA	14aA
Control	106bB	151bC	205bC

Pooled S.E. = 19.9 (excluding time-zero controls)
Anova: treatment $p<0.001$; John Innes no. n.s.; Interaction $p<0.05$ (ex. time-zero controls).

Percentage dry weight allocation to leaves is not significantly affected by submergence or nutrient level (Table 10.12). Petiole allocation is significantly lower in the control seedlings compared with the submerged ones (Table 10.12). Root allocation is lowered by submergence and is significantly affected by nutrient level and an interaction effect between submergence and JI level (Table 10.12).

Seedlings show a large difference in the dry weight/mm of petiole (and hypocotyl) length (Table 10.13). Submerged seedlings can have between three and four times the total petiole length of the control plants for the same petiole dry weight. This effect was independent of nutrient level. Interestingly, the dry weight/mm of petioles in the submerged plants is less than their time-zero level.

10.5.2 Discussion

RGRs of control seedlings show that R. sceleratus plants are at the top of the range quoted by Grime and Hunt (1975) for ruderal plants (sensu Grime, 1979) of 1.3 to 2.1 mg/mg/day. The reduced RGRs of 0.6 to 0.9 mg/mg/day under submerged condition shows that even under "stress" conditions seedlings of R. sceleratus can have RGRs equal to barley and maize seedlings (Grime and Hunt, 1975).

In contrast to RGRs, the NAR values are at the bottom of the range quoted by Grime and Hunt (1975) of 6.0 to 17.7 mg/mm^2/week for ruderals. However, the quoted values were maximum seedling NARs. The NARs are mid-range compared with average growing season values (for C3 dicotyledons) given by Larcher (1980) of 3.5 to 7.0 mg/mm^2/week; these values are not for seedlings.

Table 10.12

Percentage dry weight allocation to organs (mean and S.E. per plant) for R. sceleratus plants in experiment 5 (n= 5).

(a) Leaves and cotyledons

Treatment	John Innes number 1	2	3
Time-zero control	58.9 (3.4)a**	55.7 (5.2)a	59.8 (3.0)a
Submergence	60.0aAB*	61.2aB	58.6aAB
Control	59.2aAB	55.5aAB	50.8bA

Pooled S.E. = 3.1 (excluding time-zero controls)
Anova: treatment n.s; John Innes n.s.; Interaction n.s. (ex. time-zero controls).
** different lower case superscript means significantly different at $p<0.05$ (t-test) from the time-zero controls alone.
* different upper case superscript means significantly different at $p<0.05$ using pooled S.E. in t-test (see Mead and Curnow, 1983) (ex. time-zero controls).

(b) Petioles and hypocotyl

Treatment	John Innes number 1	2	3
Time-zero control	27.8 (3.5)a**	28.8 (4.2)a	27.1 (2.9)a
Submergence	28.8aBC*	31.5aC	31.5aC
Control	22.3aAB	22.0aAB	18.8bA

Pooled S.E. = 2.6 (excluding time-zero controls).
Anova: treatment $p<0.001$; John Innes n.s.; Interaction n.s. (ex. time-zero controls).

(c) Roots

Treatment	John Innes number 1	2	3
Time-zero control	13.4 (1.6)a**	15.5 (3.3)a	13.1 (1.9)a
Submergence	11.3aA*	7.3bB	7.7bB
Control	18.6bB	22.5bB	30.54bC

Pooled S.E. = 1.8 (excluding time-zero controls).
Anova: treatment $p<0.001$; John Innes no. $p<0.025$; Interaction $p<0.001$ (ex. time-zero controls).

Table 10.13

Dry weight per mm of petiole length (mg/mm, mean and S.E. per plant) for *R. sceleratus* plants in experiment 5 (n= 5).

Treatment	John Innes number 1	2	3
Time-zero control	1.28 (0.09)[a]**	1.17 (0.16)[a]	1.28 (0.19)[a]
Submergence	0.51 (0.11)[b]	0.63 (0.05)[b]	0.66 (0.06)[b]
Control	2.05 (0.13)[c]	2.15 (0.22)[c]	1.92 (0.17)[c]

** different lower case superscript means significantly different at $p<0.05$ (t-test) from the time-zero controls alone.

Root dry weights and dry weight allocation to roots were the only factors to show an overall significant effect of nutrient level. The nutrient effect interacts with submergence for root dry weights but with root allocation there is both an interaction with submergence and an independent effect of nutrient level.

In Chapter 8 a strategy involving the following tactical changes in response to submergence in R. repens was put forward: increased petiole length, reduced petiole number, reduced dry weight/unit length for petioles and increased allocation to petioles. All the elements of this strategy can be seen in R. sceleratus seedlings following submergence.

10.6 Overall Discussion

Going back to the question at the end of section 10.5: Why do JI3 plants show no submergence treatment effects on allocation?

Taking the original answers in order:

1. Higher nutrient levels during the submergence treatment prevent, or compensate for, any allocation differences that occur at lower nutrient levels.

Nutrient level affected the dry weight of roots and root allocation but these effects are complicated by an interaction with submergence. Within the submergence treatment there are no significant differences between the three nutrient levels. This hypothesis is not supported by the results of this experiment.

2. Higher nutrient levels after submergence treatment enable plants to compensate for dry weight changes during submergence.

Higher nutrient levels from submergence until harvest must explain the disappearance of the submergence effects in the JI3 plants.

R. sceleratus plants are often associated with nutrient rich conditions and areas likely to be seasonally submerged (Fitter, 1978). It may be that submergence limits the distribution of this species to nutrient rich areas.

The above discussion is concerned with the lack of allocation changes in JI3 plants following submergence. However, several floral characters did show significant changes in the JI3 plants following submergence. This may be related to the structural changes in the flowering stem that resulted from submergence. In non-submerged plants the basal rosette of leaves was easily distinguished from the leaves of the flowering stem but in the submerged plants this distinction was not present.

The reason for this may be related to the elongation of the lower stem internodes between the rosette leaves in the submerged plants. Samarakoon and Horton (1981) submerged well developed rosettes of R. sceleratus and found that these lower stem internodes elongated following submergence. The submergence of seedlings may affect the later development of these stem internodes.

Another structural difference between submerged and control flowering stems was the reduction in branching in the submerged plants. This was probably the reason for the reduction in seed heads/plant. Again there is evidence for seedling submergence affecting later development.

10.7 Summary

1. Submergence of R. sceleratus as seedlings results in a delay in both flowering and seed production.

2. In the JI1 and 2 treatments submergence resulted in significant differences in dry weights and dry weight allocations to organs. This was not the case however for JI3 plants.

3. The JI3 plants did show significant effects of submergence with floral characteristics, as did the JI1 and 2 plants.

4. All submerged plants showed an increase in the number of seeds/seed head. This to some extent compensates for the reduction in seed heads/plant.

5. The loss of a submergence effect on dry weights and dry weight allocations in JI3 plants is probably related to the increased nutrient levels influencing growth after submergence. This may be related to the fact that R. sceleratus is associated with nutrient rich areas.

Chapter 11

Seed Production and Submergence in Ranunculus sceleratus

"Common in and by slow streams, ditches and shallow ponds of mineral-rich water with a muddy bottom" (Clapham et al, 1962:76) of R. sceleratus.

11.1 Introduction

Clapham et al (1962) state that Ranunculus sceleratus plants can be found growing in water. R. sceleratus plants have been observed growing in water for much of the year in a ditch at Port Meadow, Oxford (S.J.Smith, pers. obser). However, observations on these long term submerged plants suggested that these rarely survived to flowering (see Chapter 12). R. sceleratus seeds will, however, germinate underwater (see Chapter 13) and seedlings will survival considerable periods of submergence (see Chapter 12).

The following question was of interest in this experiment:

Can R. sceleratus flower after long term submergence and, if it can, what effect does this have on the timing of flowering and seed output?

Unlike all other experiments in this thesis the submergence treatment was not short term but for most of the experiment. This was designed to represent the extreme condition of plants growing in water.

11.2 Experimental Results

Young seedlings of R. sceleratus were either grown in air or submerged for the whole of the experiment (see section 2.4 under experiment 7).

As a result of petiole extension the leaves of the submerged plants reached the surface of the water 5 days after submergence. The leaves produced floated on the surface and were never lifted above it, even though the petioles developed considerable "slack". The petioles produced underwater did not carry fully expanded leaves until they reached the water surface. The leaves produced by the submerged rosettes were never of the normal "crowfoot-type" produced by the control rosettes, but remained the "heart shaped-type" of the first true leaves.

The control plants produced flowering stems on average 26 days after the start of the experiment, whereas the submerged plants produced their flowering stems on average 18 days later (after 44days). The flowering stems produced by the submerged plants were much shorter than the control plants and were not branched; the stems of the controls were highly branched. The flowering stems of the submerged plants bore their flowers (with the peduncle attached directly to the main stem) and also a few aerial "crowfoot-type" leaves just above the water surface

Flowers were produced on average 35 days after the start of the experiment by the control plants whereas the submerged plants on average produced flowers after 49 days (14 days later). Seed production was also delayed in the submerged plants (Figure 11.1). The number of seed heads/plant, the number of seeds/plant and the number of seeds/seed head produced by the submerged plants was much less than for control plants

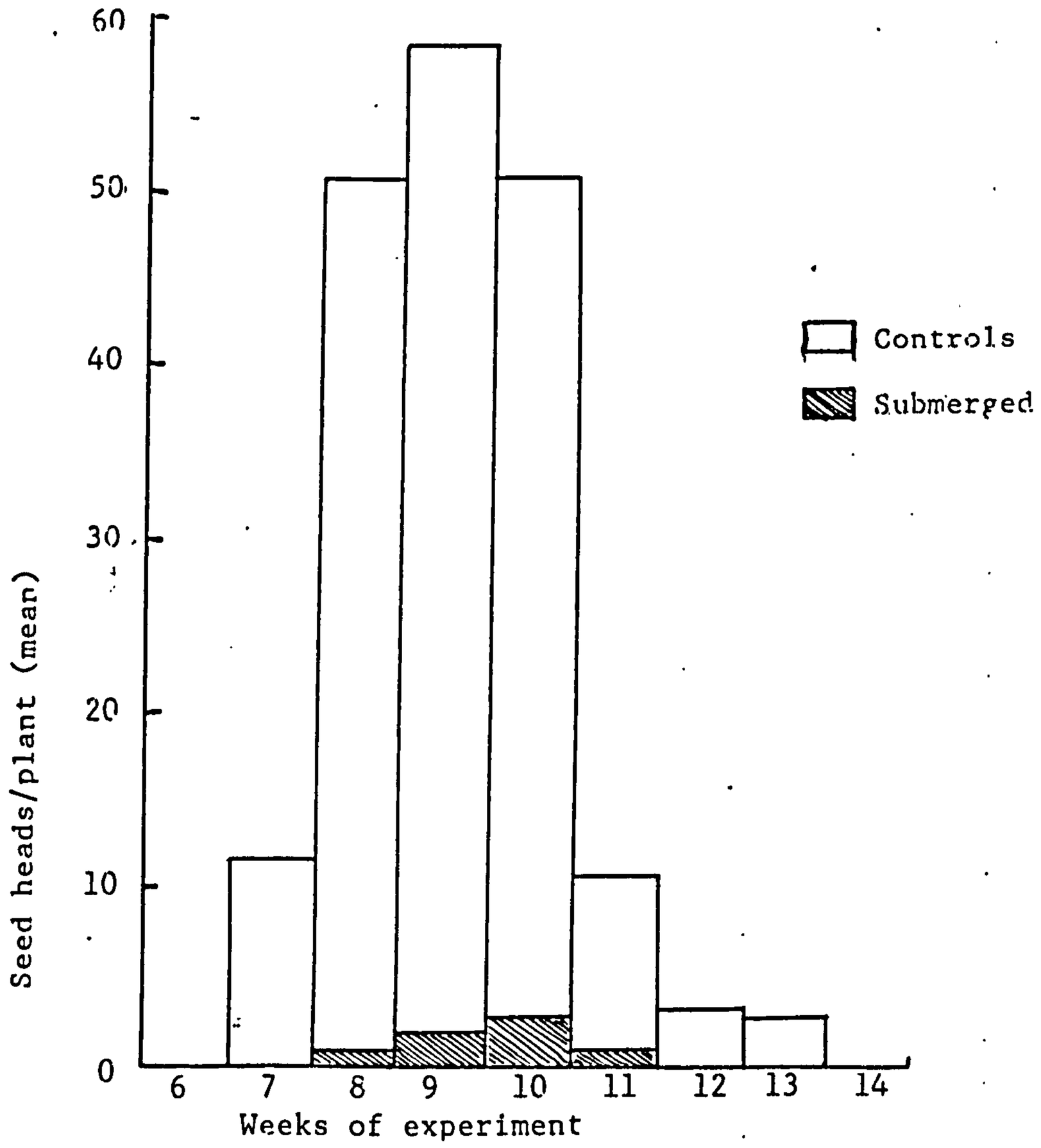


Figure 11.1

The production of ripe seed heads with time by R. sceleratus plants in experiment 7.

(Table 11.1). However, mean seed weights were not significantly different between the two treatments (0.12mg for both).

11.3 Discussion

Samarakoon and Horton (1981) submerged 16 week old plants of R. sceleratus and found that the flowering stem elongated to leave the flowers just above the water surface. They made no measurements of flower or seed production, but did note the unbranched form of the flowering stem in the submergence treatment. This reduction in branching very probably resulted in a reduction in the number of flowers /plant (see Chapter 10).

Samarakoon and Horton (1981) suggest that the rapid elongation response of the stem precludes the development of laterally inserted flowers and that stem growth is limited to the three basal internodes, which results in a less branched flowering stem. This implies a direct "cost" of the submergence response by flowering stems in the number of flowers (and therefore probably seeds) per plant.

As in the one week submerged plants, submergence resulted in a delay in flowering. The time delay was of the same order in both cases. The submerged plants were also smaller throughout the experiment. The delay in flowering may be size related, as suggested in Chapter 10 for the one week submerged plants.

Although submergence did not affect mean seed weight, it did however, result in large reductions in the number of seeds/seed head. This is in marked contrast to the one week submerged plants (Chapter 10) which

Table 11.1

The number of seed heads, total seed weight, the number of seeds, seeds per seed head and mean seed weight (mean and S.E. per plant) for *R. sceleratus* plants grown in experiment 7 (n = 3).

	Treatment	
	Control	Submergence
Seed heads	190.0 (15.4)^{a**}	4.7 (3.3)^{b}
Total weight of seed (g)	2.37 (0.6)^{a}	0.30 (0.2)^{b}
Number of seeds	19700 (4700)^{a}	250 (170)^{b}
Seeds/seed head	102 (16.3)^{a}	54 (1.1)^{b}
Mean seed weight (mg)	0.12 (0.01)^{a}	0.12 (0.01)^{a}

** different superscript means significantly different at $p<0.05$ (t-test).

showed an increase in the number of seeds/seed head.

This experiment shows that R. sceleratus plants will flower even after long term submergence but fecundity is severely reduced.

11.4 Summary

1. Long term submergence of R. sceleratus plants greatly affects flowering and seed production.

2. Submerged plants show delayed flowering and considerable reductions in the number of seed heads/plant and the number of seeds/plant.

3. Mean seed weight, however, was unaffected by submergence.

Chapter 12

The Demography of Ranunculus sceleratus with Special Reference to Submergence

"The annual plant's life history is unique because the actively growing fraction of the population must be derived each year from the seed bank"

(Klemow and Raynal, 1983)

12.1 Introduction

Ranunculus sceleratus is a species of unpredictable habitats being common on disturbed wet ground or mud on the margins of lakes, rivers and ponds and therefore subject to submergence and drought. According to Toorn (1980) R. sceleratus can act as a summer or winter annual, but Salisbury (1970) indicates that it may also be a "biennial". Bakker et al, (1966), however, consider R.sceleratus an ephemeral species with no true seed dormancy, seeds over-wintering because of low temperatures.

The lack of seed dormancy recorded by Bakker et al (1966) is in contrast to many reports of seed dormancy in this species (Toorn and Hove, 1982; Salisbury, 1970; Mayer and Poljakoff-Mayber, 1975). There is virtually no information concerning survivorship (Toorn (1980) states that 0.01% of seeds reached the flowering stage) and none for the pattern of survivorship within the year.

A study of the demography of this species was carried out with the

following questions in mind:

1. Are there any patterns in emergence?

2. What are the patterns of survivorship?

3. Do survivorship and emergence patterns affect fecundity?

4. How does submergence influence survival and fecundity?

5. Can an overall demographic strategy be outlined?

12.2 Demographic Results

R. sceleratus plants were mapped from 3 December 1982 until the 4 August 1984 at approximately 14 day intervals (see section 2.4 under demographic study). The study site was a drainage ditch on the edge of Port Meadow, Oxford (see Appendix 2). Mapping was conducted along three transects running down the bank of the ditch perpendicular to the water's edge (these transects are termed A, B and C). Each transect was divided into ten quadrats numbered from 1 to 10 from the top of the bank (Figure 12.1).

12.2.1 Initial Mapping

The initial mapping took place on the 3 December 1982. The three quadrat 10s were not mapped because they were under water. The rosettes mapped were of a mixed, unknown age composition but they were divided

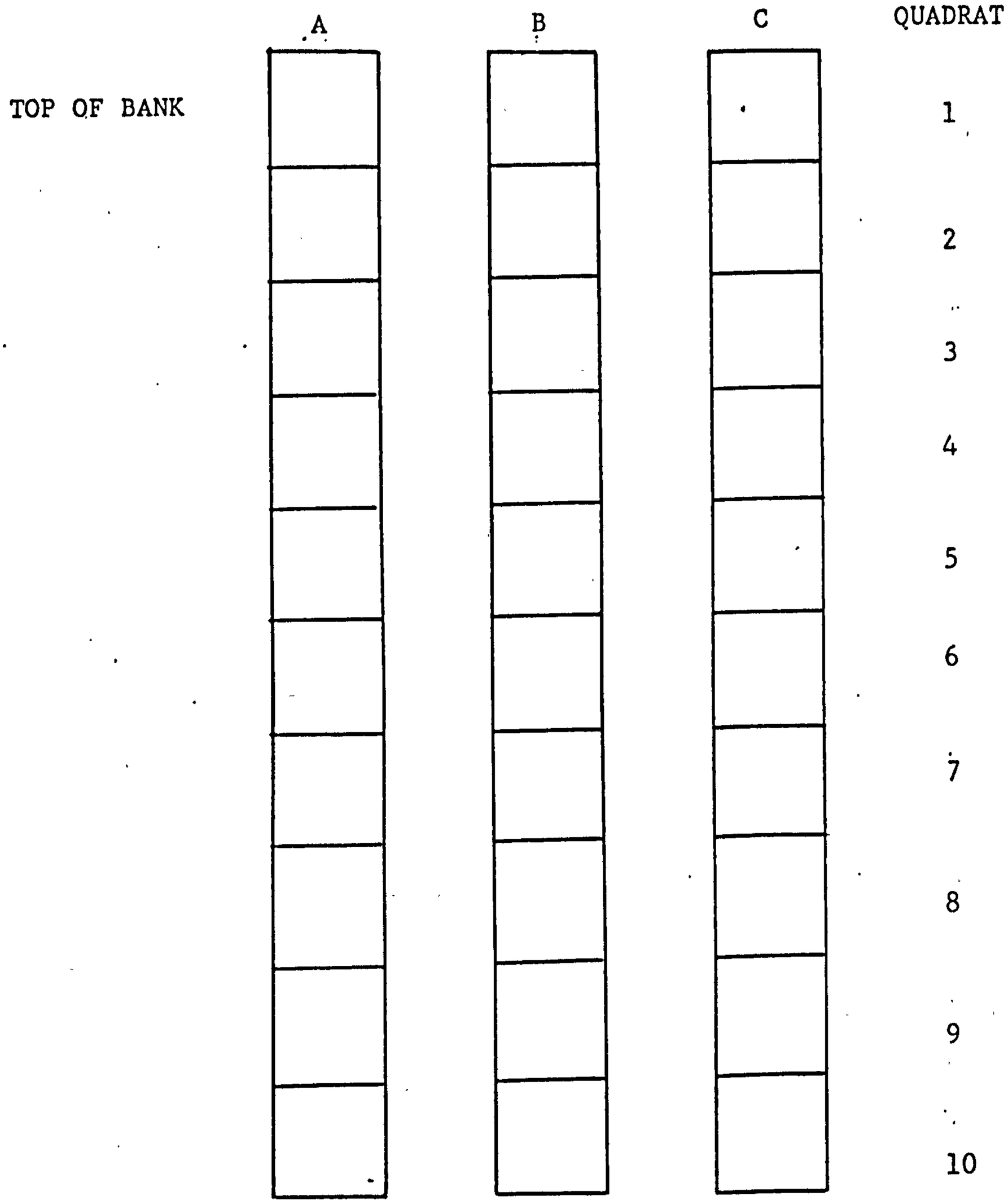


Figure 12.1

The layout of quadrats at the Port Meadow ditch site for the *R. sceleratus* demographic study.

into five size classes (Table 12.1).

The rosette diameter classes form two distinct groups, those rosettes above 5cm diameter and those below 2cm diameter. The distribution of these plants along the transects was not even; for example, no R. sceleratus plants were found above quadrat 4 (Figure 12.2). Apart from one rosette in quadrat 6, all rosettes above 5 cm in diameter were found in quadrats 8 and 9. Ten of the thirteen extra large rosettes were in quadrat 9 (Figure 12.2). Small rosettes were fairly evenly scattered, as were seedlings apart from a very high number in quadrat 6 (Figure 12.2). The possible origins of these plants will be discussed later. The quadrat 10s, which were not mapped, contained several large rosettes.

12.2.2 Seedling Emergence

There are seasonal trends for periods of peak seedling emergence; peaks occur in autumn (September - December) and spring (April - May) (Figure 12.3). The autumnal peak is clearly the period of maximum emergence, with four to five times the number of seedlings emerging during this period relative to the spring peak.

However, emergence is not confined to the peaks but continues for much of the year (Figure 12.3). The lack of emergence during summer 1983 and 1984 was probably due to a lack of soil water due to low rainfall (see Appendix 2) and high insolation. The absence of emergence in January/February 1984 was due to mapping not being possible because of deep water over the site. Observations suggested that little, if any, emergence took place underwater at this time (but see Chapter 13).

Table 12.1

The number of R. sceleratus rosettes, based on rosette diameter at 3/12/82 at the Port Meadow ditch site.

Diameter (cm)	n	Description
<1	184	Seedlings
1-2	18	Small rosettes
2-5	0	Medium rosettes
5-10	24	Large rosettes
>10	13	Extra large rosettes

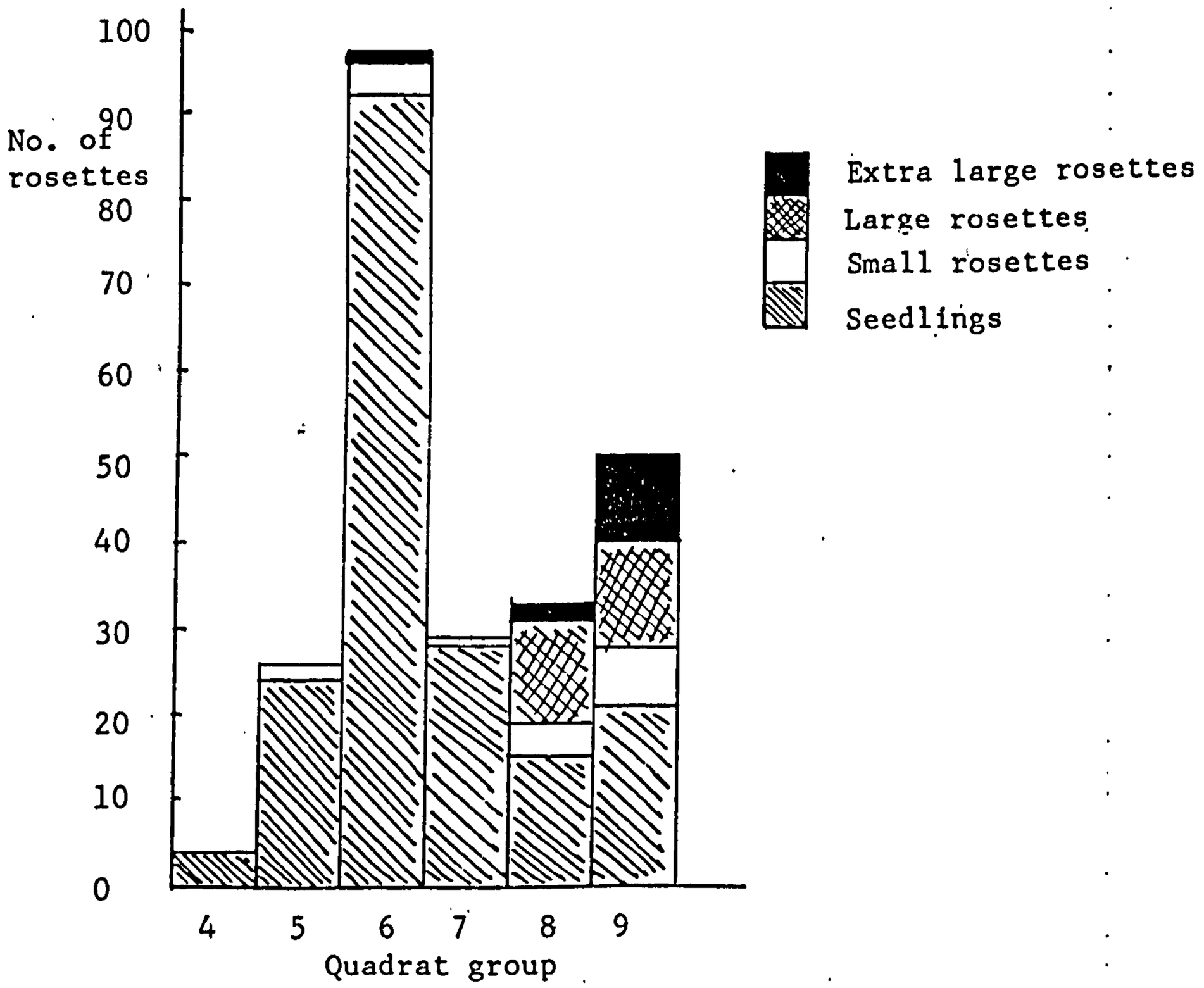


Figure 12.2

The distribution of the original rosettes (3.12.82) by quadrat group at the Port Meadow ditch site.

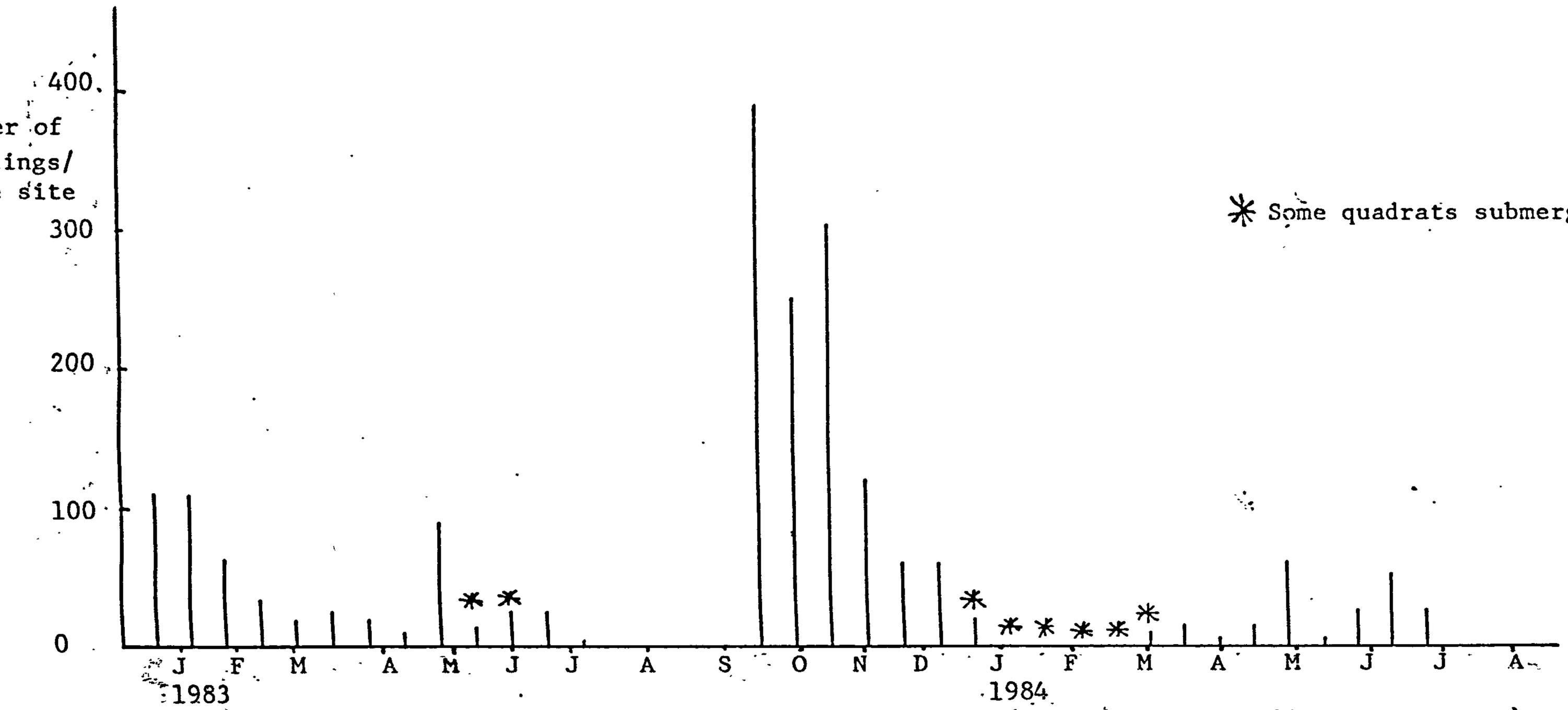


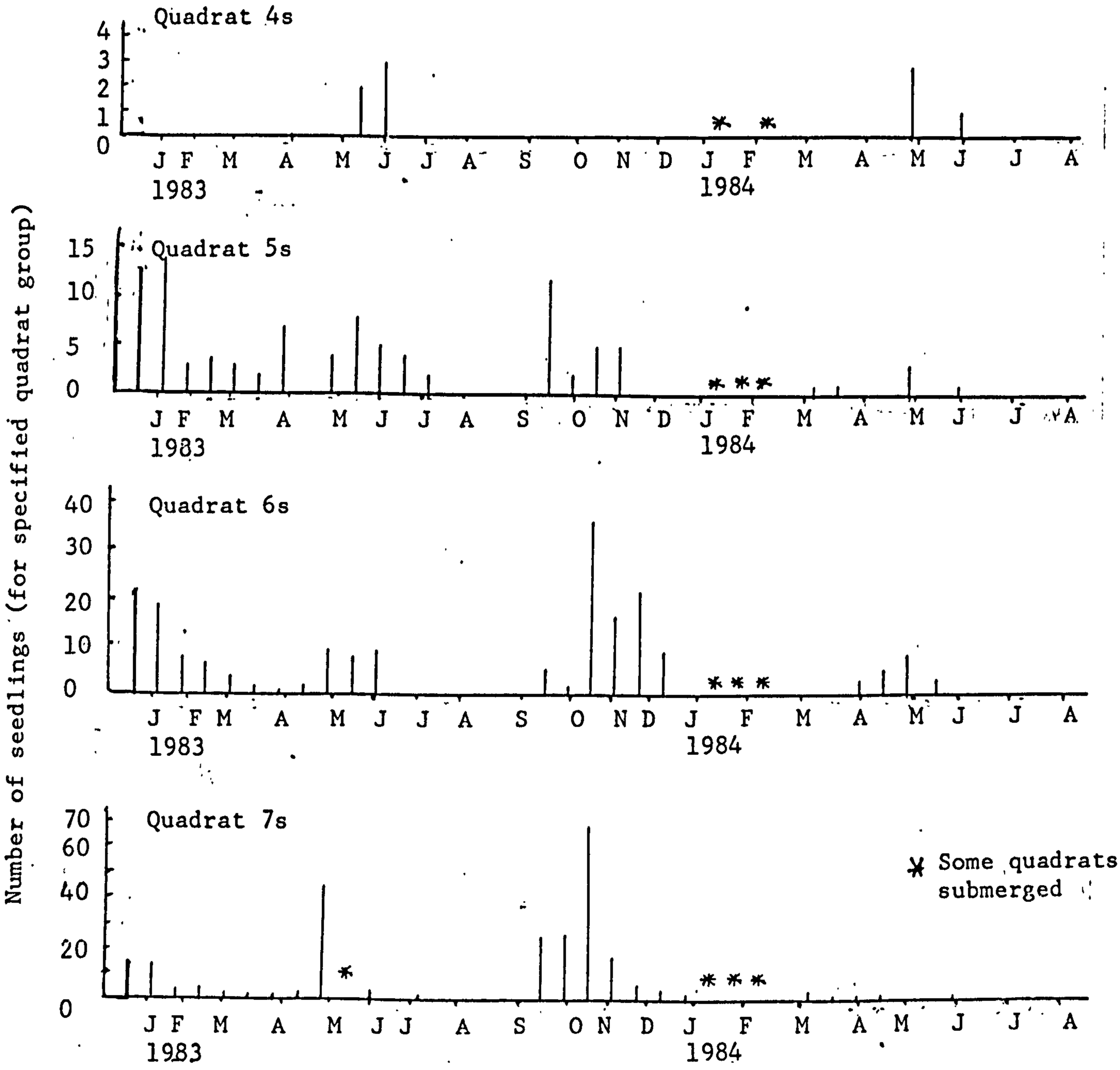
Figure 12.3 Time / months, starting at 3.12.82. (Visits at approx 14 day intervals)

The emergence of R. sceleratus seedlings with time (20.12.82 to 4.8.84) at the Port Meadow ditch site.

The pattern of emergence for each of the quadrat regions (cumulative for the three transects) is similar to the overall pattern but with some interesting differences (quadrats 1 to 3 are excluded because no emergence took place in these quadrats) (Figure 12.4). The timing of emergence peaks is very similar apart from a later autumn peak in quadrat regions 6 and 7 and no obvious spring 1984 peak in quadrat region 7. One over-riding feature of these emergence patterns is the increase in the number of seedlings emerging from quadrat regions 4 to 10, i.e. from the top of the bank down to the water's edge (Figure 12.4).

This may be related to a lack of soil moisture in the upper quadrats but also to percentage plant cover which decreases from the top of the bank to the bottom (Figure 12.5). The differences in percentage cover may be due to the wetter ground at the bottom of the transect suffering greater disturbance from livestock (horses and cattle) trampling than does the drier, upper ground. Submergence may also reduce the growth of grasses which are the main covering plants. The combined action of these factors on percentage plant cover can be seen in early 1984 during/after submergence (Figure 12.5).

Another factor affecting seedling emergence may be the seed bank. At this site emergence of R. sceleratus seedlings from the seed bank appears to be concentrated in the middle to lower bank region but the middle region sample consistently had a greater number of seedlings emerging (Table 12.2). R. sceleratus at this site has a persistent seed bank in the middle to lower quadrat regions (Table 12.3). Differences in the size of the seed bank may not be translated into differences in seedling emergence because the increased disturbance through livestock trampling experienced by the wetter, lower quadrats will result in



Time /months, starting at 13.12.82. (Visits at approx. 14 day intervals)

Figure 12.4

The emergence of R. sceleratus seedlings with time (20.12.82 to 4.8.84) by quadrat group at the Port Meadow ditch site (continued overleaf).

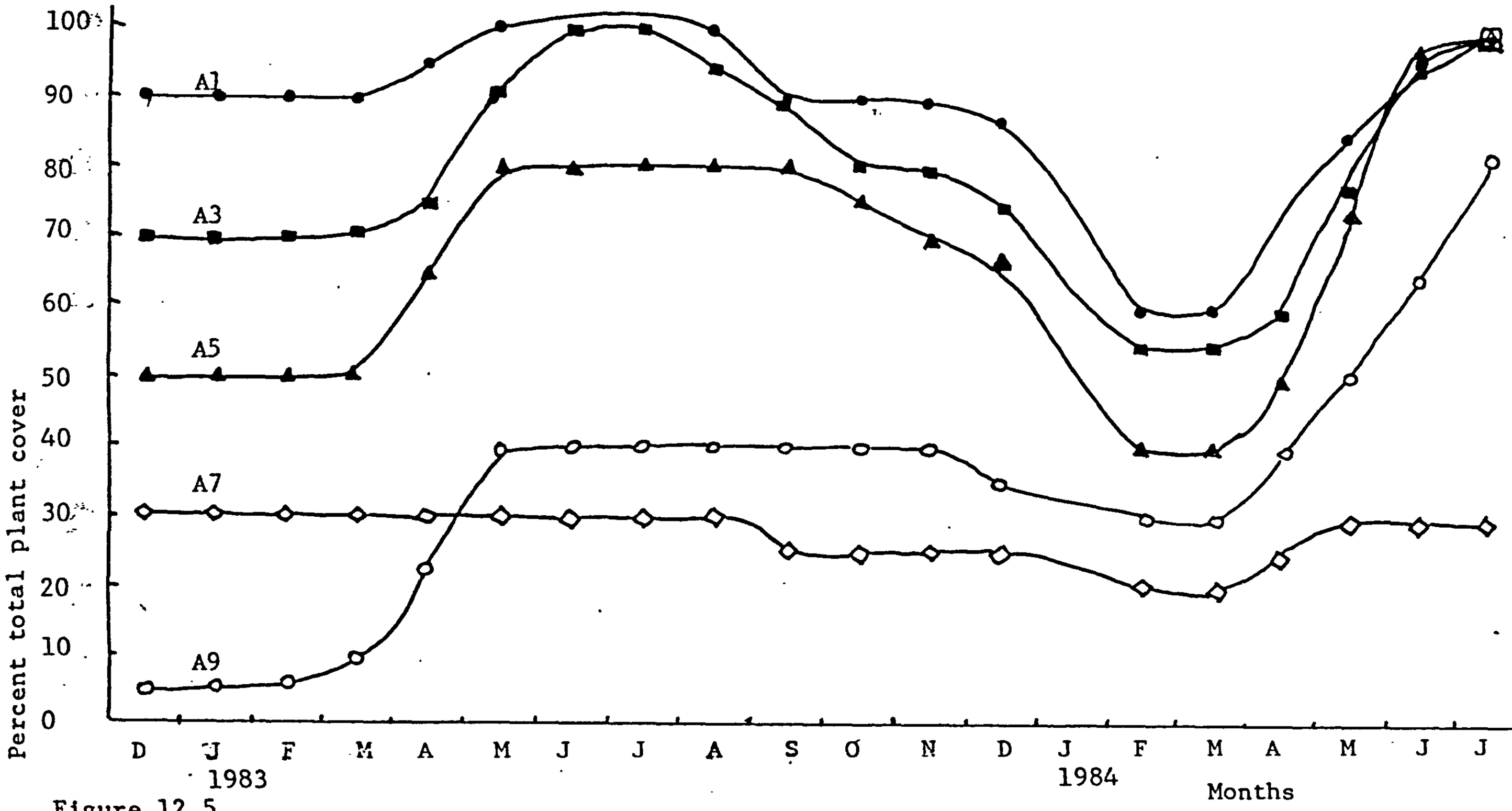


Figure 12.5

Percentage plant cover (total) with time for selected quadrats in the 'A' transect at the Port Meadow ditch site.

Table 12.2

Estimated number of germinable *R. sceleratus* seeds (mean and S.E.) in the soil at the Port Meadow ditch site 11/11/82 and 28/4/83 (based on three 5x5x3cm soil samples; see section 2.5).

Quadrat level	Seedlings/soil sample 11/11/82	28/4/83
1	0 (0)	0.7 (0.3)
5	2.0 (0.6)	7.3 (0.3)
9	1.3 (0.3)	1.0 (0.6)

Table 12.3

The presence of germinable *R. sceleratus* seeds in the seed bank with time at the Port Meadow ditch site, Nov 1982 to July 1983 (method as Table 12.2).

Quadrat level	Date 11/82	4/83	9/83	2/84	7/84
1	0	+	0	0	0
5	Y	Y	Y	Y	Y
9	Y	Y	Y	Y	Y
10	-	-	Y	-	-

0 = no seedlings in sample
+ = only 1 seedling in sample
Y = >1 seedling in sample
- = no soil collection

increased seed mobility and affect emergence in this area.

The autumn 1983 seedling emergence results were used to investigate some of these factors. Quadrats with percentage total plant cover above 65% had very low seedling emergence (<20), whereas quadrats with below 50% cover had moderate to very high seedling emergence (25-256) (Figure 12.6). The variations in seedling emergence in the quadrats with plant cover below 50% can to some extent be accounted for by variations in the seed input to the quadrats during June/July 1983 (Figure 12.6).

The relatively high seedling emergence in quadrat B9 may be because seed from two flowering plants from quadrat B8 fell into this quadrat in summer 1983. That there is limited seed dispersal is supported by the close correlation of seed input and emergence in the low cover quadrats.

Interestingly, the seedling emergence in quadrats of above 65% cover is independent of seed input, for example B4 and B5 compared to C4 and C6. It appears that above 65% cover seedling emergence is mainly "gap" limited whereas below 50% cover seedling emergence is seed limited. There are no data for the band between 50% and 65% cover so the limiting factors in this band are not known.

The role of a seed bank, other than recently added seed, can be seen in the quadrats below 55% cover which had no seed input from the last flowering period (June/July 1983). Three quadrats (C8, C7 and A7) had 26 or 27 seedlings emerging. The similarity in the numbers emerging may reflect a similar seed bank in each of the three quadrats.

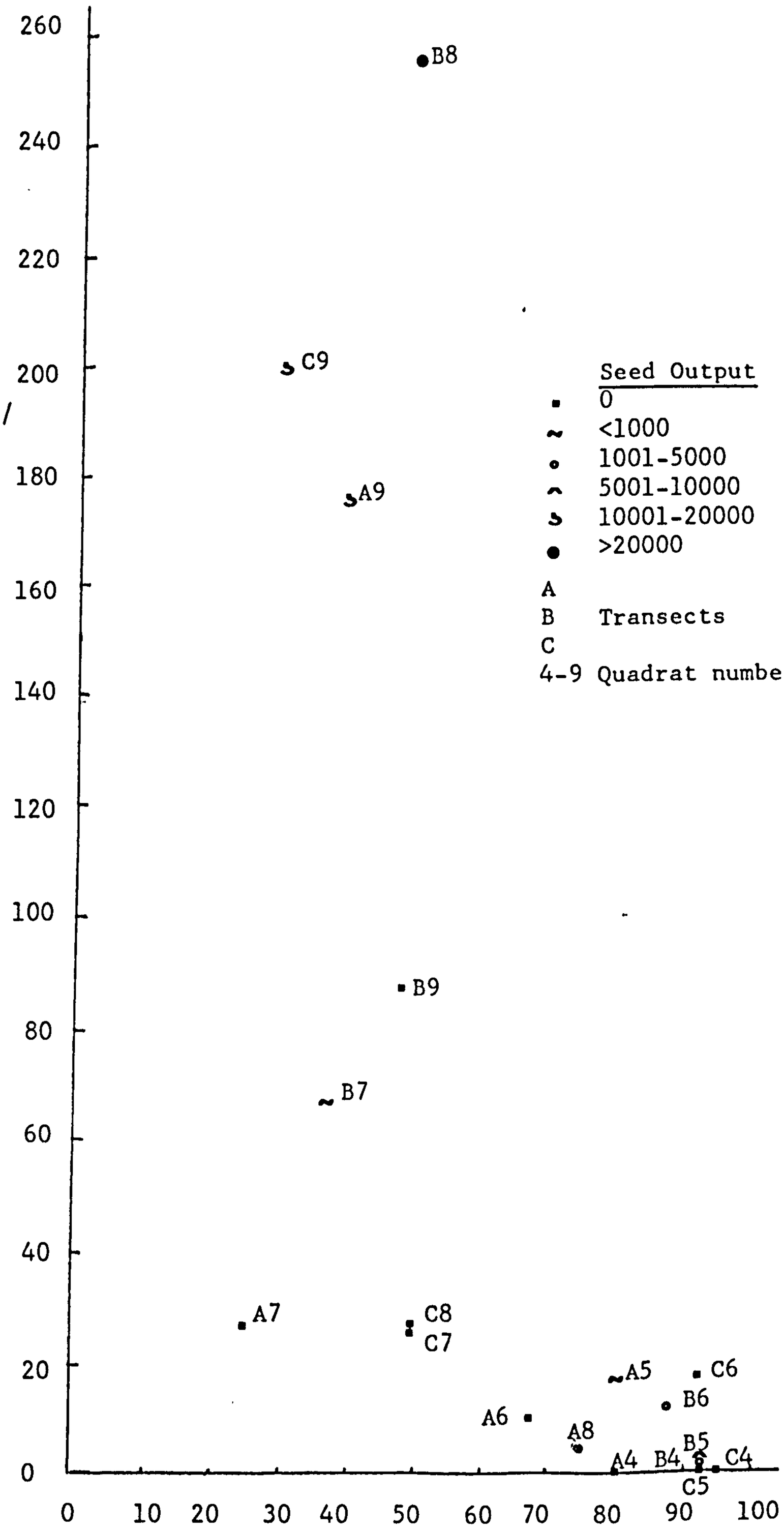


Figure 12.6

Emegence of R. sceleratus seedlings during Autumn 1983 against percentage total plant cover by quadrat (seed output by quadrat (1983) is included by the use of symbols).

12.2.3 Survivorship

The over-wintering survivorship (until 24 March 1983) of the initial rosettes (on 3 December 1982) appears to increase with rosette diameter (Table 12.4). One of the reasons for this differential winter survival based on rosette size is related to the root system of the smaller rosettes being poorly developed allowing them to be prone to frost heave (S.J.Smith pers. obser.). The older rosettes have a well developed fibrous root system, preventing the plant being pushed out by frost heave (see Regehr and Bazzaz, 1979).

The extra large and large rosettes show a much greater loss during the post-wintering period (until flowering: 20 June 1983) (Table 12.4). The reason for this may be related to the submergence that occurred during May; the larger rosettes were all found in the submerged area. The increased loss during May can be seen in the depletion curves (Harper, 1977) (Figure 12.7). The curves for the larger rosettes are very similar, whereas the small difference in rosette size between the small rosettes and seedlings gives very large differences in survivorship.

Submergence may result in plant mortality because petioles respond to submergence by elongation; the petioles produced are less rigid and susceptible to desiccation. When the water level falls these petioles and their leaves suffer desiccation and many, if not all, are lost. This loss of petioles and leaves could increase mortality.

With survivorship from flowering to seed set (6 July 1983) there was only loss of the extra large and large rosettes (Table 12.4). This differential mortality can be seen in the depletion curves (Figure 12.7). The reason for this mortality may again be related to the

Table 12.4

Survivorship (fractional) of initial R. sceleratus rosettes at the Port Meadow ditch site, based on rosette diameter class on 3/12/82 (see Table 12.1).

Rosette diameter (cm) (at 3/12/83)	Survivorship			
	Over-wintering	To flowering	To seed set	n
<1	0.12	0.07	0.07	184
1-2	0.33	0.22	0.22	18
5-10	0.63	0.25	0.13	24
>10	0.54	0.23	0.15	13

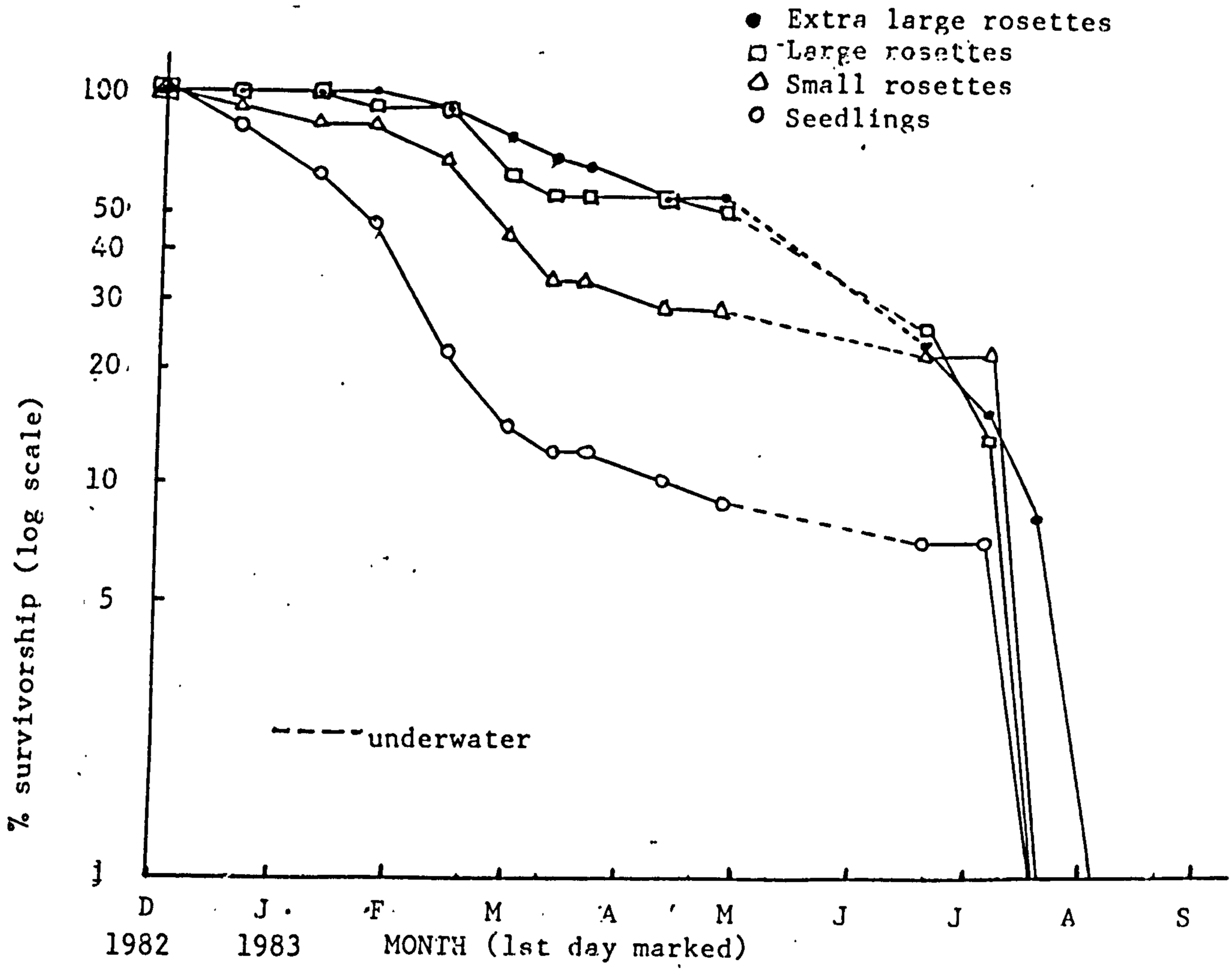


Figure 12.7

Depletion curves for the original R. sceleratus rosettes (3.12.82) based on rosette diameter (see Table 12.1) at the Port Meadow ditch site.

desiccation and loss of the previously submerged petioles.

However, much of the loss resulted from flowering stems being broken by livestock (S.J.Smith pers. obser.). The tall, hollow flowering stems are very easily snapped off at the base by the animals brushing them. There was no evidence of grazing damage, which is consistent with reports that this plant contains large amounts of acrid, probably toxic chemicals (Misra and Dixit, 1980), as do three other members of the genus Ranunculus which results in grazer avoidance (Harper, 1977).

The survivorship curves for cohorts emerging between December 1982 and August 1983 (Figure 12.8) have very similar patterns and a shape roughly corresponding to Deevey Type II (Deevey 1949) reflecting a near constant mortality rate throughout the life cycle. However, there is a trend towards a Deevey Type III survivorship pattern, that is, adults have a lower mortality risk.

The survivorship curves for cohorts emerging between September 1983 and August 1984 (Figure 12.9) show two patterns of survivorship. The curves for autumn/winter cohorts have a shape roughly corresponding to Deevey Type III curve (Deevey 1949), reflecting a decrease in mortality risk with age whereas the curves for the spring/summer cohorts have a shape roughly corresponding to a Deevey Type II curve (Figure 12.9).

Overall cohorts of R. sceleratus in this study showed survivorship curves of the Deevey Type II or III shape. There is a trend for autumn emerging seedlings to show the Deevey Type III shape and a trend for summer emerging seedlings to show a Deevey Type II shape.

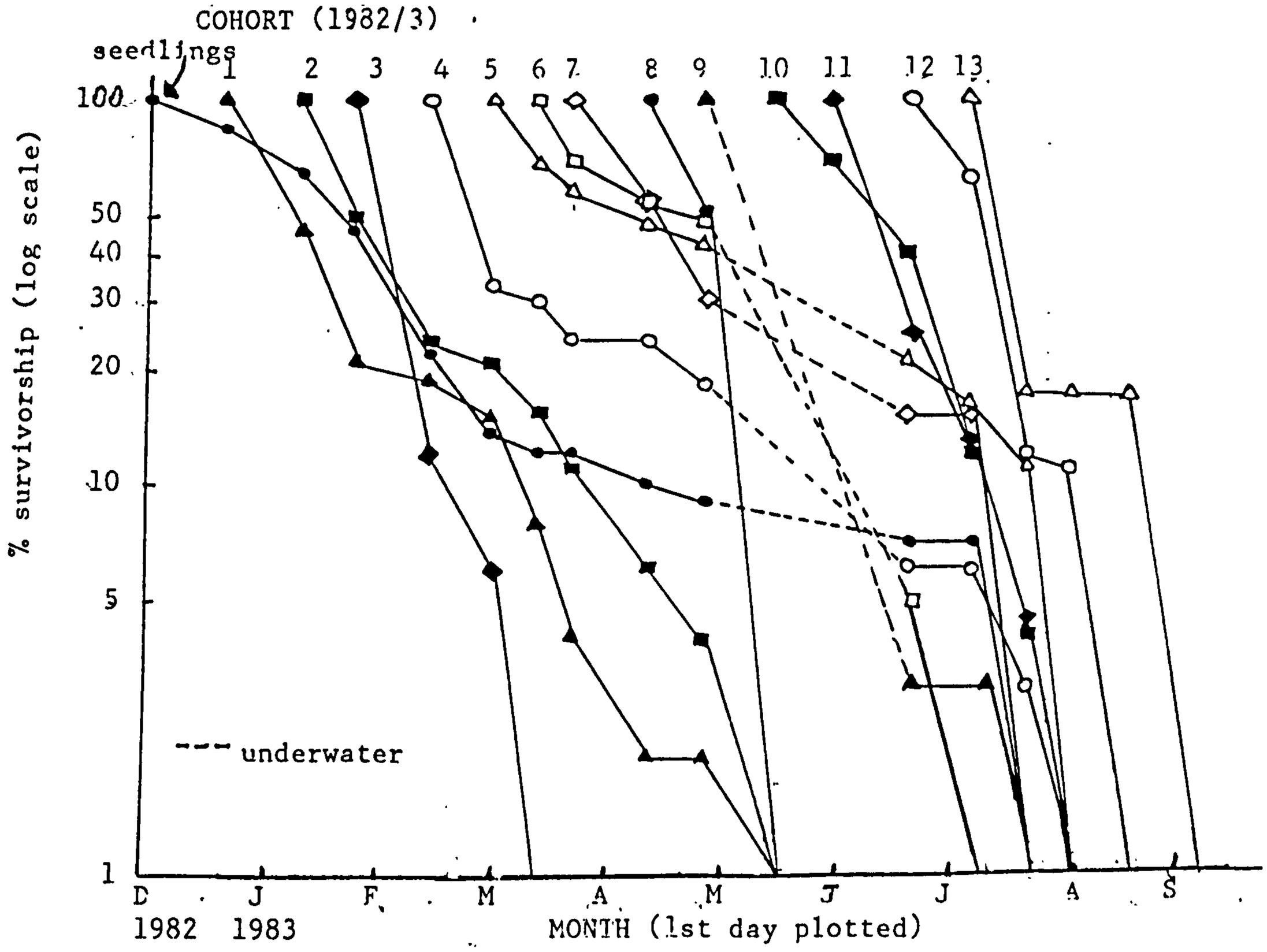


Figure 12.8

Survivorship curves for the 1982-1983 cohorts (nos. 1 to 13; 12.82-7.83) of R. sceleratus at the Port Meadow ditch site (the depletion curve of the original seedlings present at 3.12.82 is included, see Figure 12.8).

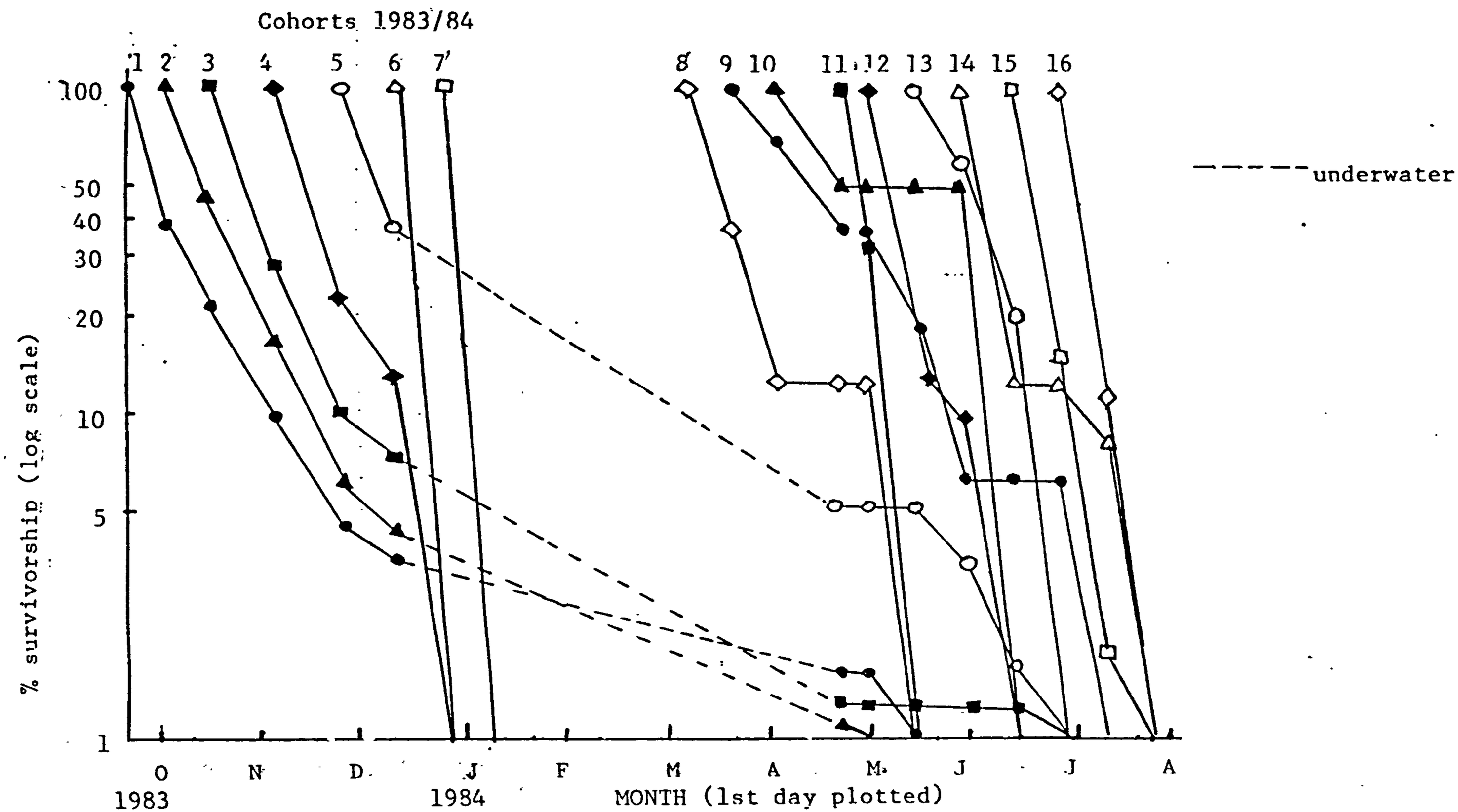


Figure 12.9.

Survivorship curves for the 1983-84 cohorts (nos. 1-16; 9.83-6.84) of R. sceleratus at the Port Meadow ditch site.

12.2.4 Flowering and Fecundity

Flowering was observed to occur in most rosettes by 20 June 1983 (Table 12.5). There was a short delay (1 visit) in flowering shown by the May cohorts (11 & 12). The minimum vegetative period was measured as 5 weeks (in the late May cohort). However, the June and July cohorts (12 & 13) did not flower even though they were alive for 8 and 6 weeks respectively, which implies that some factor prevented flowering.

Very few plants survived to flowering in 1984 possibly because of the prolonged submergence period and early drought of that year. Flowering was limited to the plants of the first five cohorts (Table 12.6). Plants in the quadrat 10 region flowered in 1984 (in contrast to 1983) but these were not mapped and so their origins were unknown. A delay in flowering (1 visit) was shown by plants in the older cohorts (Table 12.6).

The first plants to flower in 1984 flowered approximately 1 month (2 visits) earlier than plants in 1983 (Tables 12.5 & 12.6). The submergence period that occurred in May 1983 may have delayed flowering. This is supported by the appearance of a crown of raised, central leaves in several rosettes, indicative of imminent flowering stem elongation, during late April 1983.

The height of the flowering stem produced by R. sceleratus plants is related to plant size and plant age. The extra large, large and small rosettes present at the initial mapping in December 1982 produced the tallest flowering stems (40 cm to 53 cm) (Figure 12.10). The seedlings present at the initial mapping produced shorter flowering stems and showed a large range of heights (10cm to 35 cm) (Figure 12.10).

Table 12.5

Flowering date of initial *R. sceleratus* rosettes and subsequent cohorts in 1983 at the Port Meadow ditch site.

Initial rosette class or cohort	Date first marked	Flowering date
Extra large rosettes	3/12/82	20/6/83
Large rosettes	3/12/82	20/6/83
Small rosettes	3/12/82	20/6/83
Seedlings	3/12/82	20/6/83
Cohort 1	20/12/83	n/s
Cohort 2	12/1/83	n/s
Cohort 3	27/1/83	n/s
Cohort 4	15/2/83	20/6/83
Cohort 5	3/3/83	20/6/83
Cohort 6	15/3/83	20/6/83
Cohort 7	24/3/83	20/6/83
Cohort 8	13/4/83	n/s
Cohort 9	28/4/83	20/6/83
Cohort 10	17/5/83	6/7/83
Cohort 11	31/5/83	6/7/83
Cohort 12	20/6/83	n/s
Cohort 13	6/7/83	n/s

n/s= no plants survived to flowering.

Table 12.6

Flowering date of *R. sceleratus* cohorts emerging from autumn 1983 to summer 1984 at the Port Meadow ditch site.

Cohort	Date first marked	Flowering date
1	17/9/83	24/5/84
2	30/9/83	24/5/84
3	12/10/83	9/6/84
4	3/11/83	9/6/84
5	22/11/83	9/6/84
6 to 16	8/12/83 to 23/6/84	n/s

n/s= no plants survived to flowering.

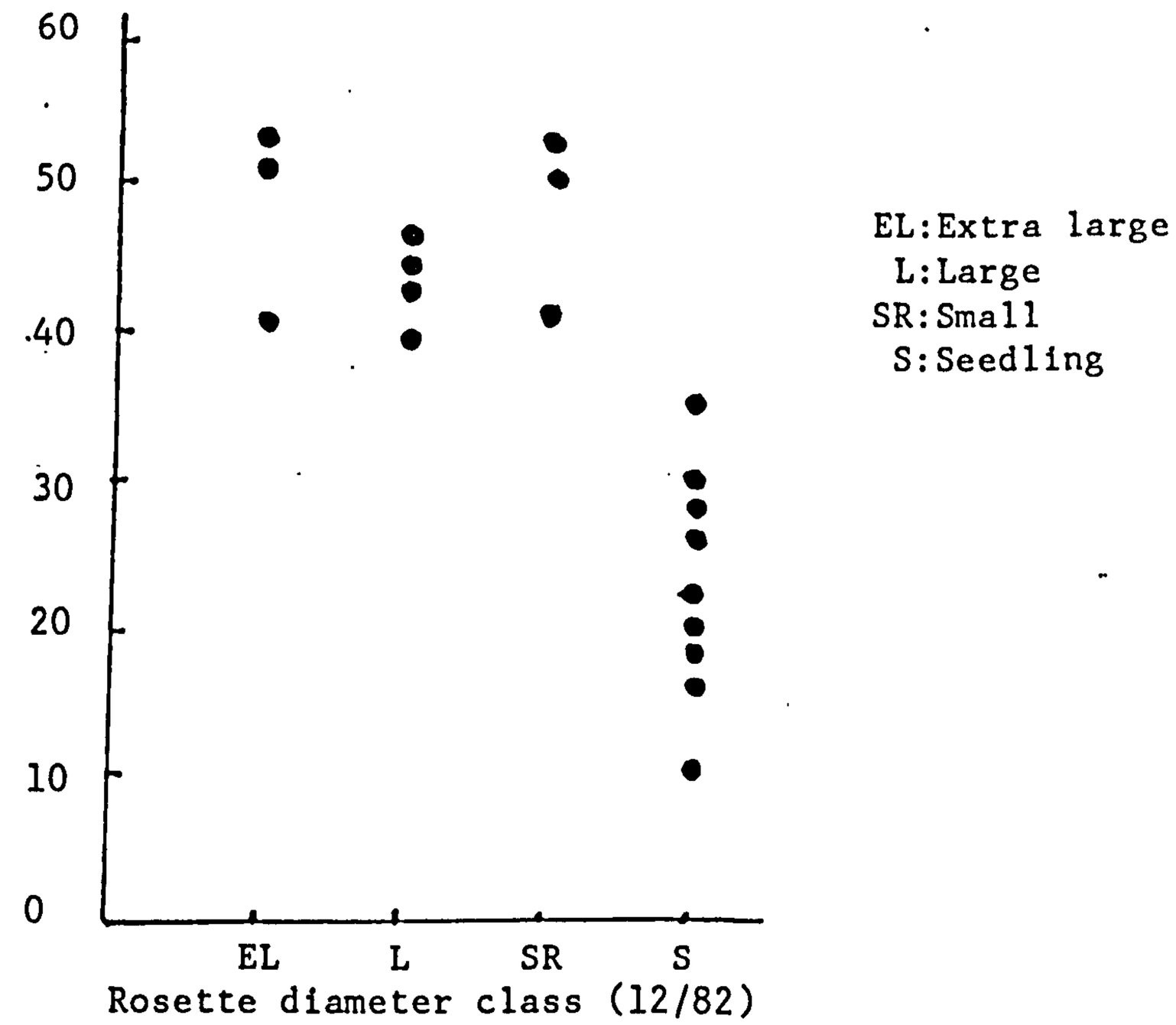


Figure 12.10

Height of flowering stem for the original R. sceleratus rosettes (3.12.82) by rosette diameter class at the Port Meadow ditch site.

With the exception of the late May cohort (11), plants from the 1983 cohorts had similar flowering stem heights (10 cm to 21 cm) (Figure 12.11). The late May cohort (11) plants, the final cohort to flower in 1983, produced flowering stems of between 5 cm and 7 cm high (Figure 12.11). The 1984 results also suggest that age is an important factor in the height of the flowering stem (Figure 12.12). These results suggest a trend of younger rosettes producing shorter flowering stems.

There was a poor relationship between pre-flowering rosette diameter and flowering stem height in 1983 (Figure 12.13) but there was a trend towards the rosettes of larger diameter producing taller flowering stems. The 1984 results also show a poor correlation between rosette diameter and flowering stem height (Figure 12.14) but the same trend of greater flowering stem height with greater pre-flowering rosette diameter.

Shorter flowering stems have fewer branches, and as flowers, and therefore seeds, are mainly borne terminally on these branches it is not suprising that seed output/plant increases with increasing flowering stem height (Figure 12.15). However, seed output is not simply a function of the height of the flowering stem because the younger rosettes which produced shorter flowering stems also had fewer seeds/seed head (Table 12.7).

The initial rosettes made a relatively large contribution to the total 1983 seed ouput compared with the later emerging cohorts (Figure 12.16). In 1984 the total seed output was due solely to plants of the initial five autumn cohorts (Figure 12.17). These results show the importance, in terms of seed production, of plants that emerge in the year before they flower; they contributed 92% and 100% of the total seed output in

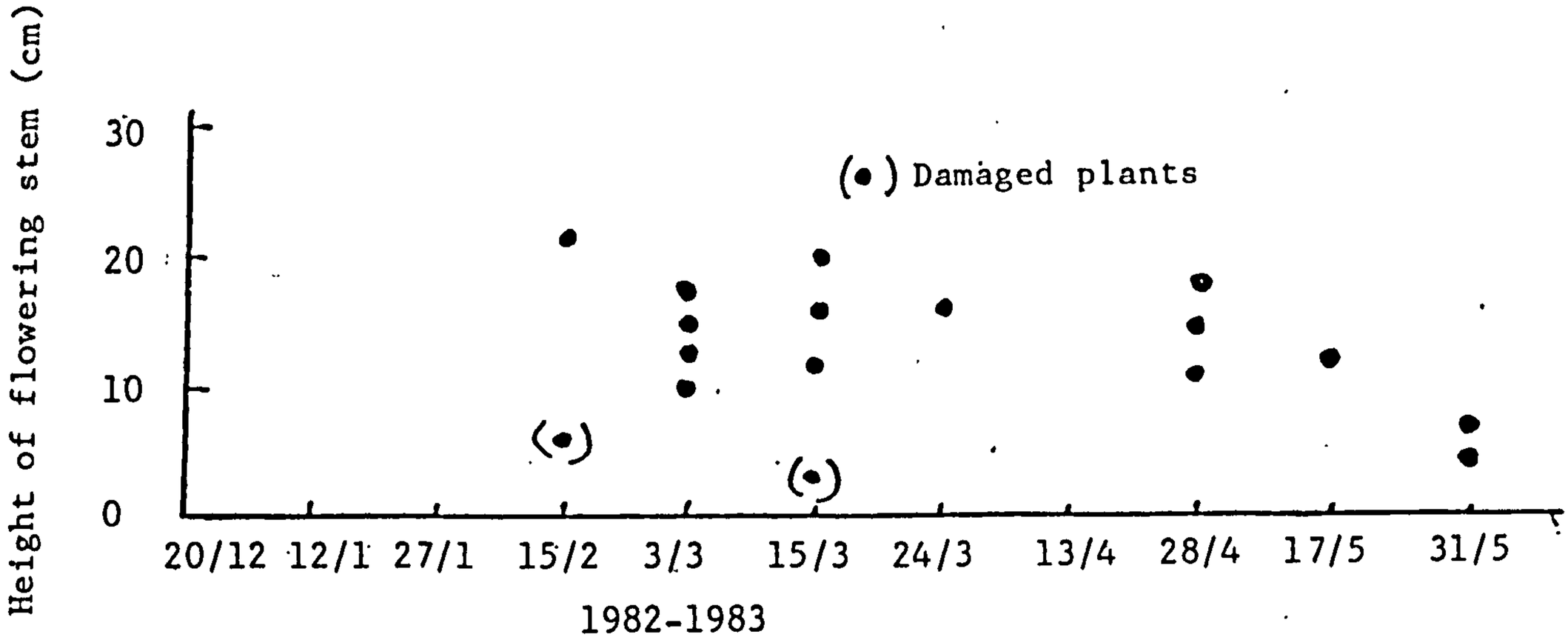


Figure 12.11

Height of flowering stem for the 1982-83 cohorts (nos. 1-13; 12.82-5.83) of R. sceleratus at the Port Meadow ditch site.

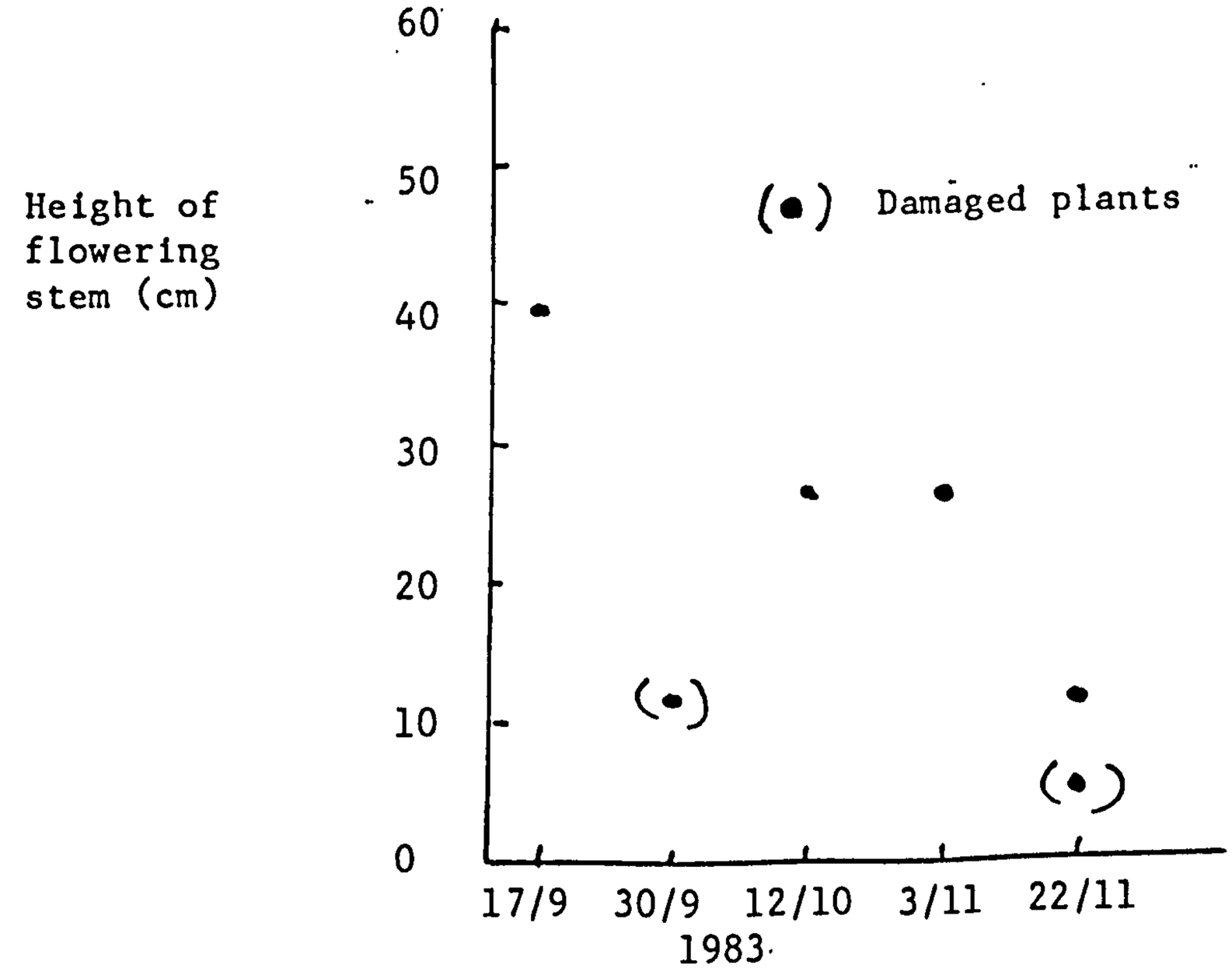


Figure 12.12

Height of flowering stem for the 1983-84 cohorts (nos. 1-5; 9.83-11.83) of R. sceleratus at the Port Meadow ditch site.

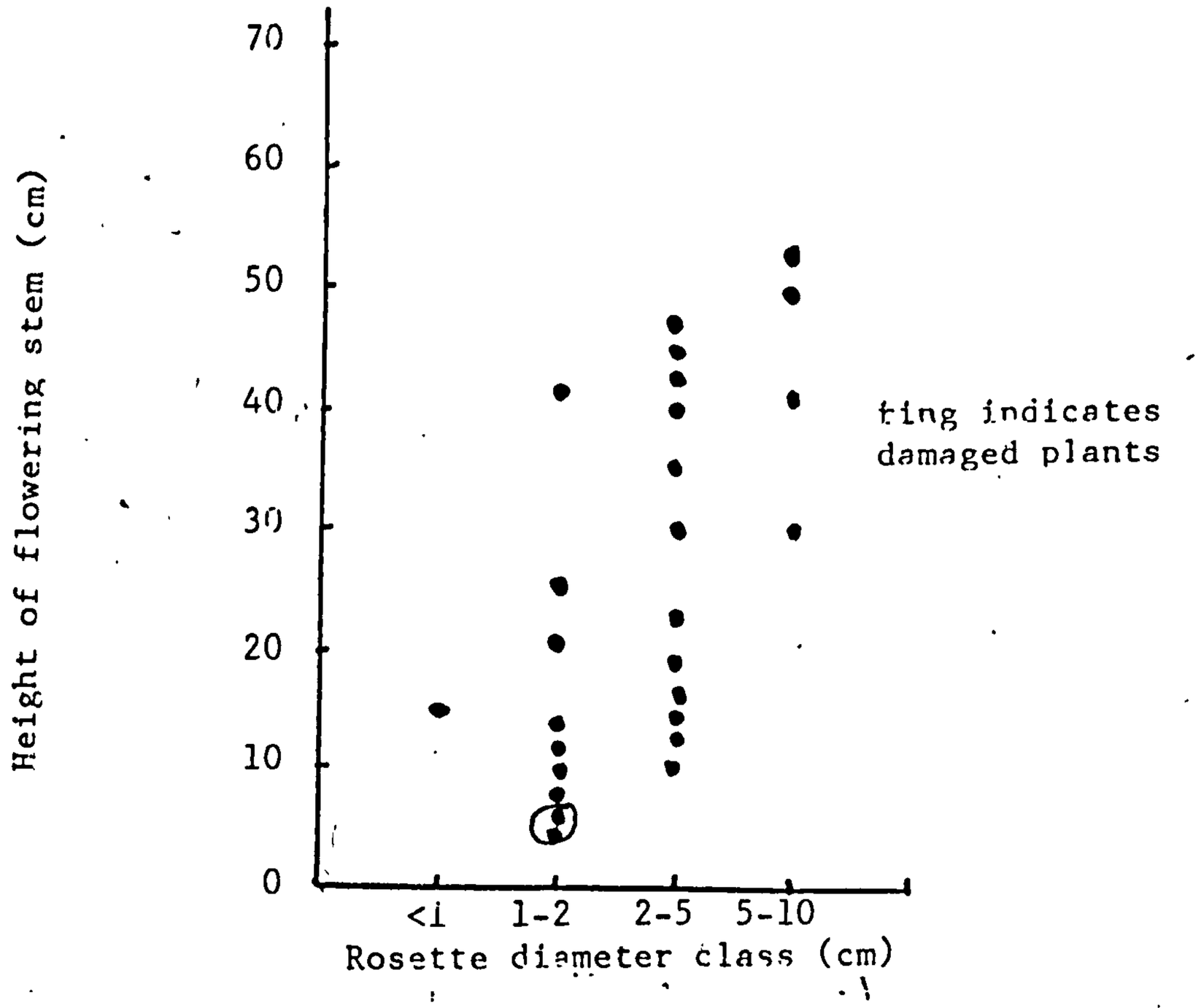


Figure 12.13

Height of flowering stems for all the R. sceleratus plants flowering in 1983 plotted against rosette diameter class immediately before flowering.

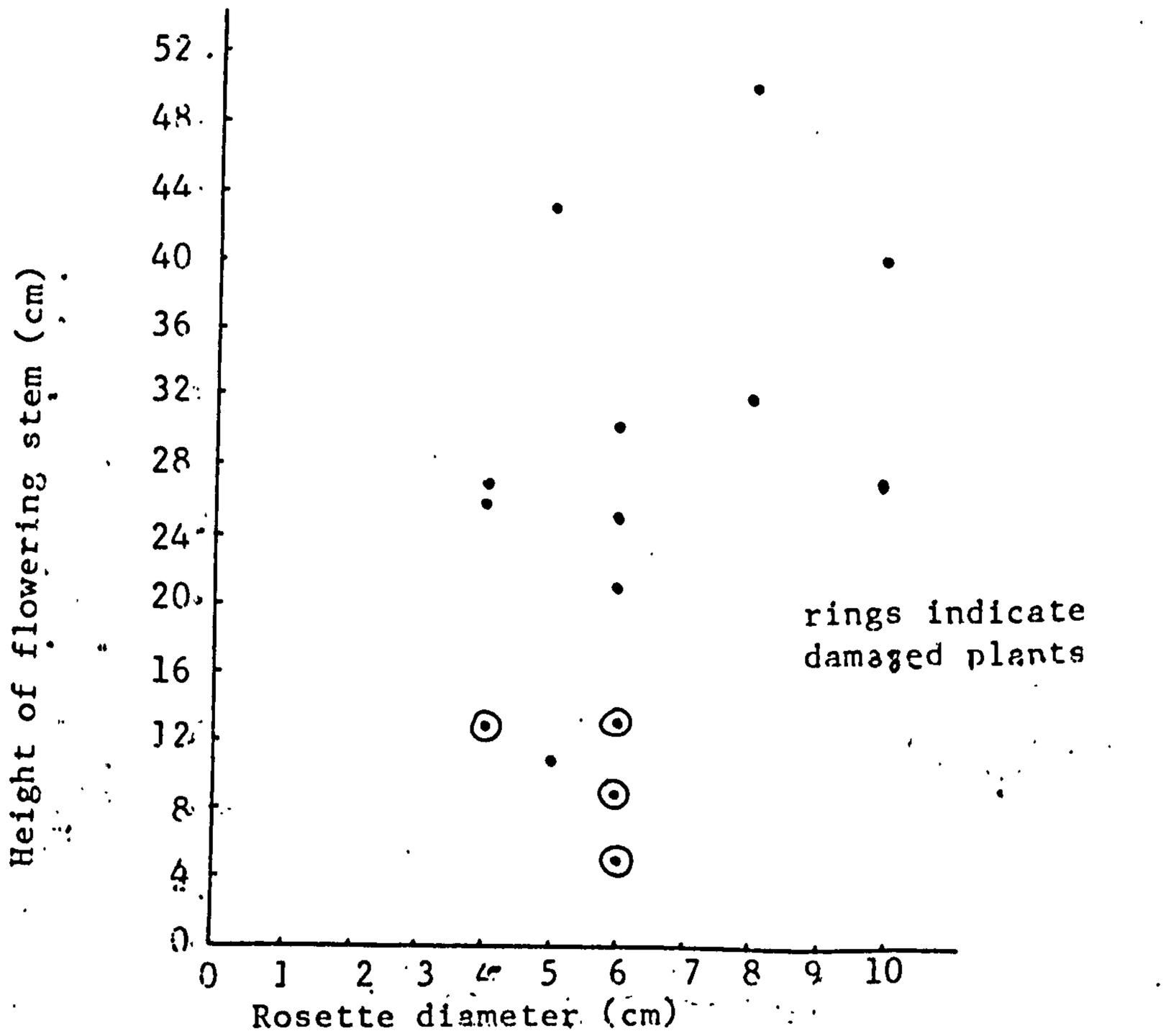


Figure 12.14

Height of flowering stems for all the R. sceleratus plants flowering in 1984 plotted against rosette diameter immediately before flowering.

Table 12.7

The number of seeds/seed head (mean and S.E., per plant) for R. sceleratus initial rosettes and later 1983 flowering cohorts at the Port Meadow ditch site.

Plants	n	Seeds/seed head
Initial rosettes	26	117 (2)a**
Later cohorts	17	78 (1)b

** different superscript means significantly different at $p<0.05$ (t-test).

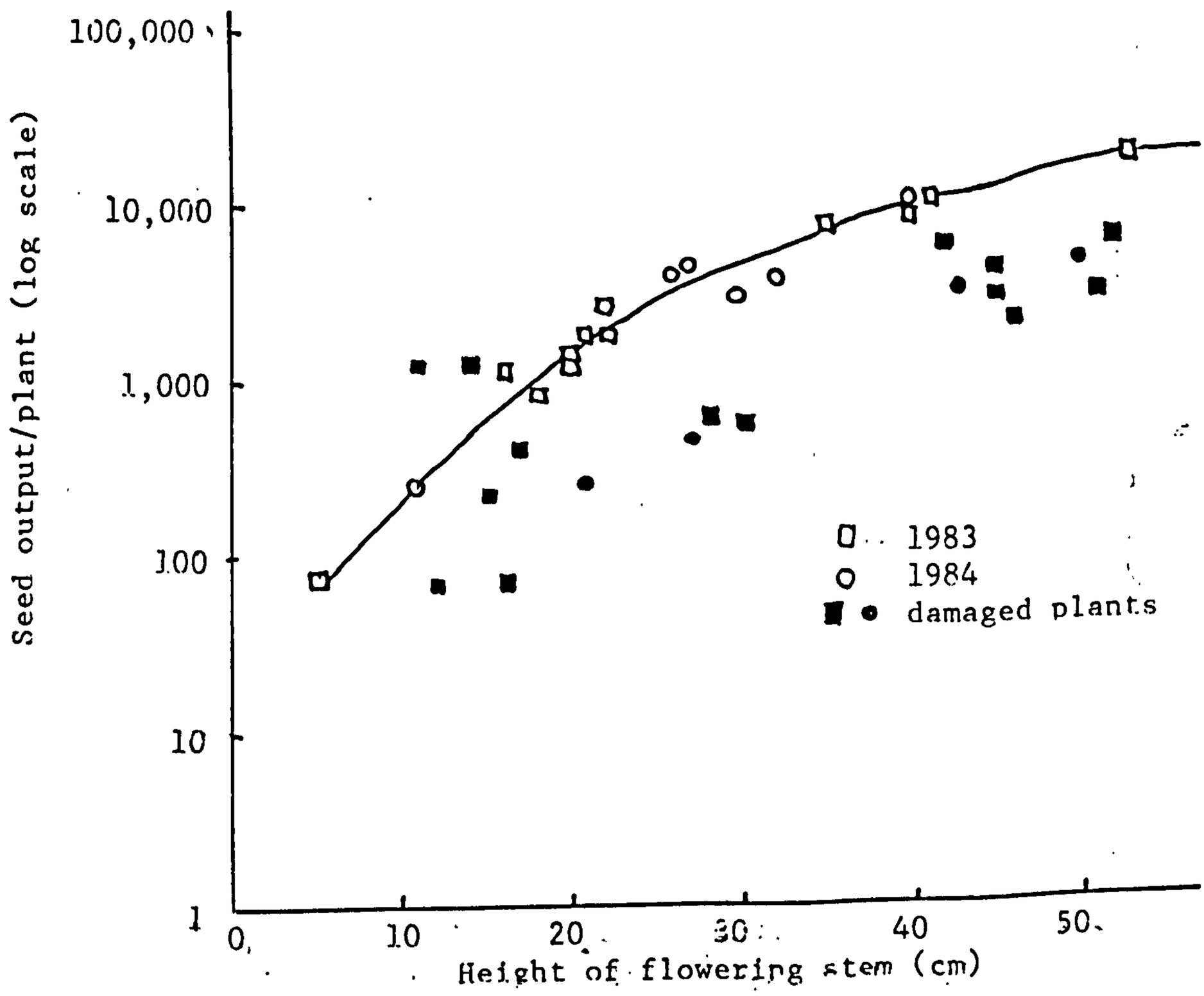


Figure 12.15

The number of seeds per plant (log scale) plotted against height of flowering stem for all R. sceleratus plants flowering at the Port Meadow ditch site.
(Line fitted by eye and excludes damaged plants).

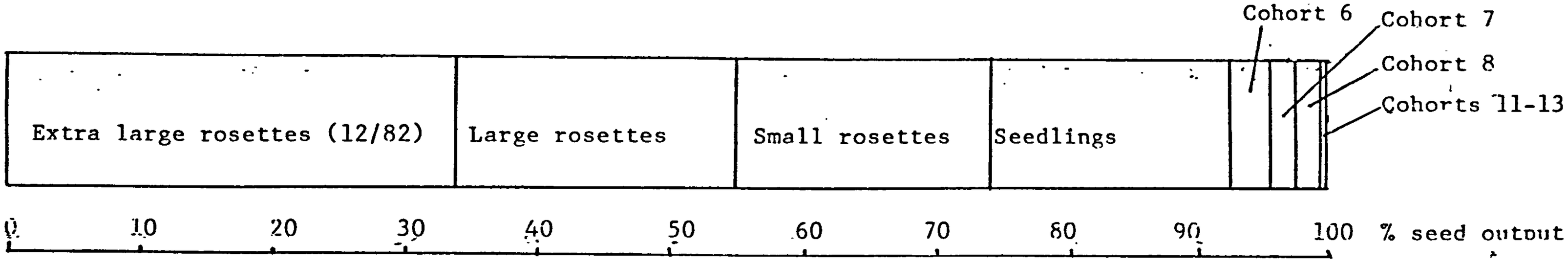


Figure 12.16

The contribution (by percentage) of the original rosettes (3.12.82) and later cohorts to the 1983 seed output from the quadrats at the Port Meadow ditch site (100% = 79,820).

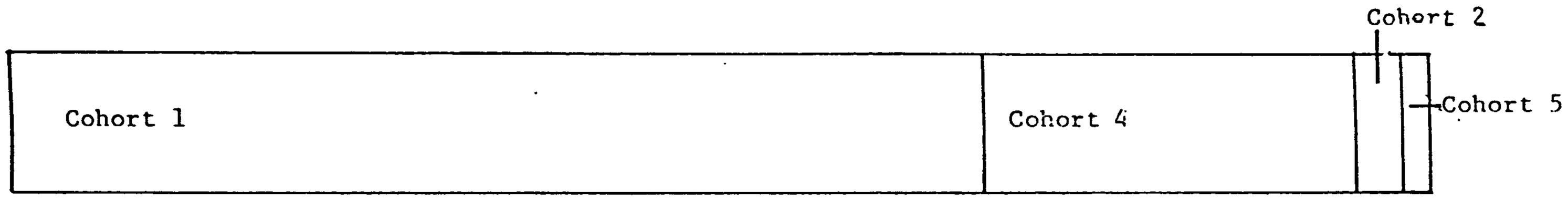


Figure 12.17

The contribution (by percentage) of each 1983-1984 cohort to the 1984 seed output at the Port Meadow ditch site (100% = 13,930; excluding 19,000 from quadrat 10 plants of unknown age).

the two years of this study.

The distributions of flowering plants in the two study periods with respect to quadrat region are very different (Figure 12.18a & b). Not only were there flowering plants in quadrat 10s only in 1984 but there were only flowering plants in the quadrats 1-8 in 1983. One of the reasons for the lack of flowering plants in the upper quadrats was that plants were lost because of the early drought in April/May 1984, the drought was more severe further up the transect (S.J. Smith pers. obser.).

Although quadrat 10 plants were not mapped (see section 12.2.1) observations were made on plants in these quadrats, the most submerged plants of the transect. No rosettes in quadrat 10s survived to flowering during 1982-1983 season but several did survive to flowering in the 1983-84 season. This may have been due to the water level falling earlier in the year in 1984 (April in 1984 c.f. July in 1983).

12.2.5 Submergence and Mortality

Survivorship by quadrat region during the prolonged submergence period of the winter 1983-1984 (Table 12.8) shows that the plants subject to the most prolonged submergence had the greatest survivorship. A possible explanation of this result is that the submerged rosettes were protected from frost by the covering water.

An alternative explanation is that these results (Table 12.8) confound differences in mortality with submergence based on age and/or size. Survivorship based on age during this submergence period (Table 12.9)

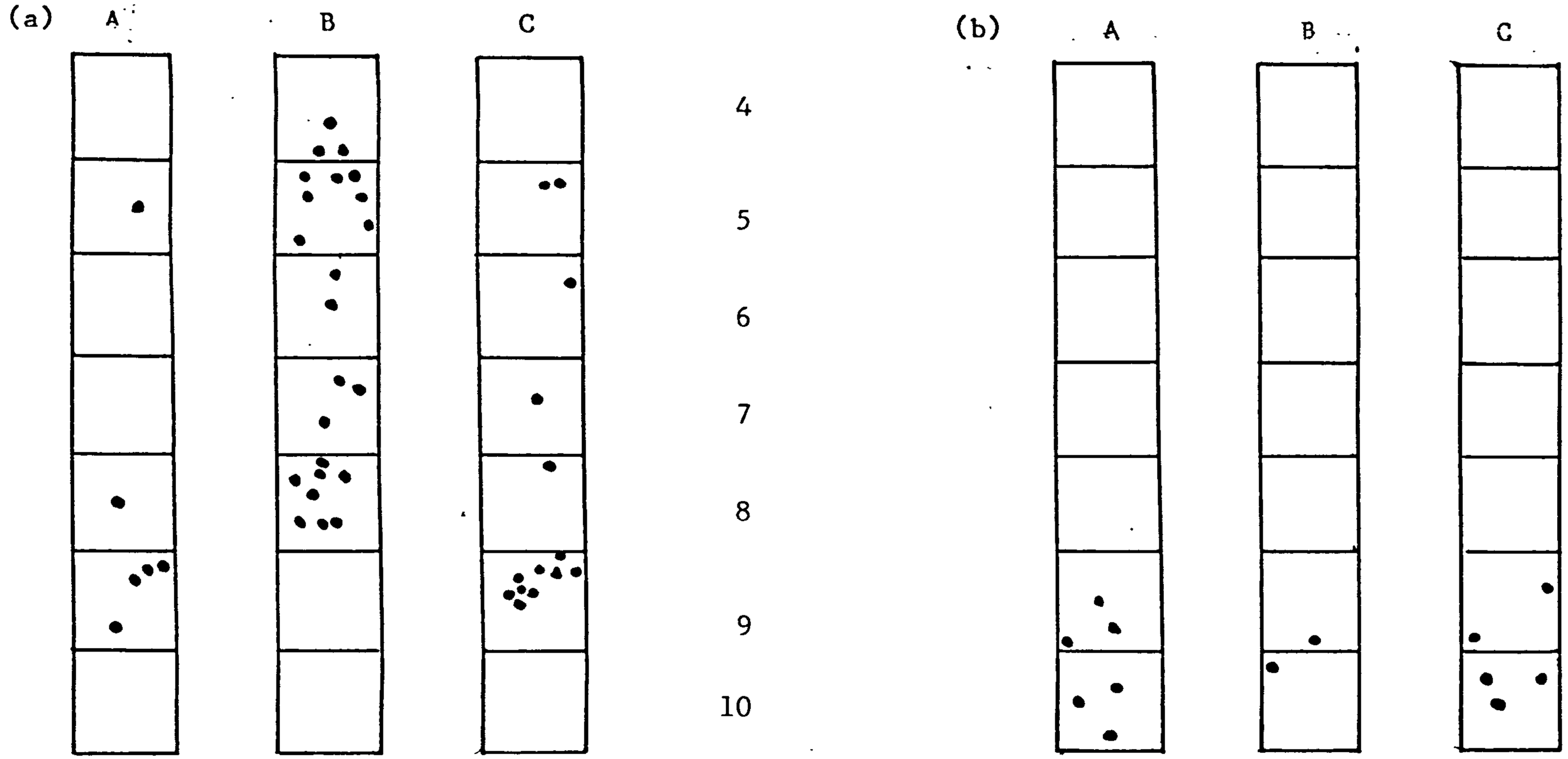


Figure 12.18

The distribution of flowering plants of R. sceleratus at the Port Meadow ditch site; (a) 1983; (b) 1984.

Table 12.8

Survivorship of autumn/winter 1983 *R. sceleratus* cohorts (1-5) during a spring submergence period by quadrat region.

Qradrat region	n	Pre-submergence	Submergence	Post-submergence
5	24	0.04	0.00	0.00
6	62	0.18	0.00	0.00
7	143	0.11	0.01	0.00
8	335	0.05	0.01	0.00
9	549	0.03	0.03	0.01

Table 12.9

Survivorship of *R. sceleratus* cohorts germinating before May 1983 during a spring submergence period based on cohort age.

Cohort	n	Survivorship
1	12	0.75
2	10	0.60
3	10	0.30
4	7	0.57
5	14	0.36
6	20	0.00
7	14	0.00

shows increased mortality of very young rosettes but no correlation between age and survivorship in the older cohorts. However, there is a strong correlation between pre-submergence rosette diameter and submergence survivorship (Table 12.10), with increased survival with increased diameter.

In May 1983 the study site could be divided into a submerged zone (quadrat 7s and lower) and non-submerged zone (quadrat 6s and higher). Survivorship during May 1983 within these two zones based on age (Table 12.11) shows that within each there is a trend towards increased survivorship with increased age. There is also a trend for increased mortality in the submerged zone but the cohort 5-7 plants do not conform to this pattern.

The same data analysed in terms of pre-submergence rosette diameter show a much stronger correlation between mortality and submergence (Table 12.12). Within each zone there is a trend for increased survivorship with increased diameter but the large rosettes do not conform to this pattern. The use of narrower size classes in 1984 may explain why the correlation between size and survivorship is better in 1984 compared to 1983.

These results shows the importance of rosette diameter for survival during submergence; the larger the rosette diameter the greater the probability of submergence survival.

Table 12.10

Survivorship of *R. sceleratus* cohorts germinating before the spring 1984 submergence period based on pre-submergence rosette diameter.

Rosette diameter (cm)	n	Survivorship
<1	43	0.00
1-2	18	0.44
2-3	27	0.52
3-4	5	0.80

Table 12.11

Survivorship of *R. sceleratus* plants during the May 1983 submergence period based on age.

Age group	Survivorship			
	Non-submerged zone	n	Submerged zone	n
Initial rosettes	1.00	7	0.63	34
Cohorts 1-3	0.00	3	-	0
Cohorts 4-6	0.33	6	0.50	16
Cohorts 7-9	0.25	16	0.00	90

12.3 Discussion

12.3.1 The Initial Rosettes

Based on rosette size it is likely that the initial large and extra large rosettes emerged before the autumn peak of 1982 probably during summer 1982. This may also explain why they are concentrated in quadrats 8 and 9; these quadrats would be more likely to have sufficient soil moisture to allow for emergence and survival during summer.

The initial small rosettes were probably from the peak autumn emergence period of 1982, based on rosette diameter and flowering stem height. The initial seedlings are probably late autumn peak and post autumn peak. It is interesting that the small difference in rosette diameter between small rosettes and seedlings in December 1982 should make such differences in survival and fecundity (Table 12.13). Many authors report size dependent mortality and fecundity in a wide range of plant species (Cook, 1980; Werner, 1975).

12.3.2 Seedling emergence pattern

Several authors (Mayer and Poljokoff-Mayber, 1975; Salisbury, 1970; Whitehead, 1971) have stated that germination in R. sceleratus is promoted by diurnal fluctuations in temperature. However, diurnal fluctuations in temperature for Oxford (Figure 12.19 and see Appendix 2) and the emergence pattern (Figure 12.3) do not correspond. This may be due to the air temperatures not reflecting the temperature regime experienced by the seeds buried in the soil. Alternatively, the lack of rainfall in the summer months (see Appendix 2) may have prevented

Table 12.12

Survivorship of *R. sceleratus* plants during the May 1983 submergence period based on pre-submergence size.

Size class (cm)	Survivorship Non-submerged zone	n	Submerged zone	n
<1	0.17	18	0.00	85
1-2	0.86	7	0.43	21
2-5	0.71	7	0.60	25
5-10	-	0	0.33	9

Table 12.13

Survivorship and fecundity of the initial (3/12/82) *R. sceleratus* small rosettes and seedlings at the Port Meadow ditch site.

Size class (at 3/12/82)	Survivorship to flowering	Seed output (per plant range)
Seedlings	0.07	300-6000
Small rosettes	0.22	10000-17000

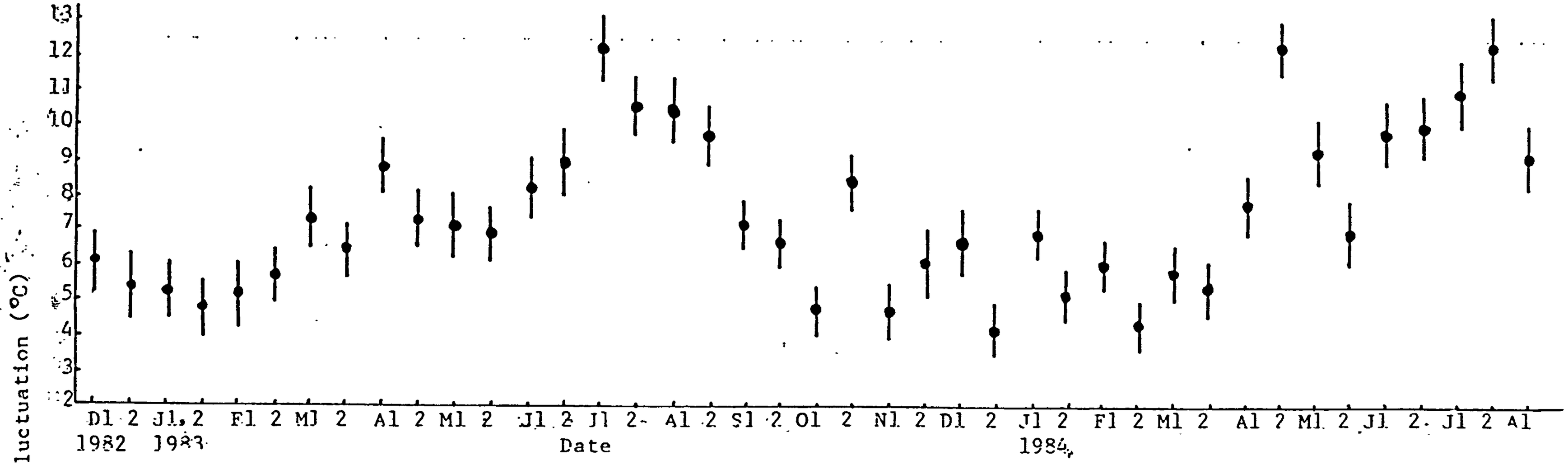


Figure 12.19

Mean daily diurnal fluctuations in temperature (with S.E.) at the Oxford Met. station (see Appendix 2) based on maximum and minimum temperatures and expressed on a half-monthly basis.

emergence when the temperature regime would otherwise have promoted germination.

The influence of rainfall, and therefore soil moisture levels, on seedling emergence can be seen at the onset of emergence in Autumn 1983 (Figure 12.20). Throughout August and September 1983 there were large diurnal fluctuations in temperature but emergence did not begin until there had been several consecutive days with rainfall (Figures 12.19 & 12.20).

Koller (1955) points out that seeds which respond to alternating temperatures usually show two emergence peaks in each year. This is the case for R. sceleratus at this site, although the spring emergence period is secondary (in terms of numbers) to the autumn emergence period.

The spread of emergence throughout the year suggests that R. sceleratus seed is polymorphic with regard to germination requirements. R. sceleratus has been shown to have polymorphic germination requirements with respect to diurnal flucuations in temperature (see Chapter 13).

Polymorphic germination is often associated with colonising species and it has been suggested that it prevents extinction through catastrophe (Harper 1965). Thompson and Cox (1978) found that the autumn and spring emergence peak in Hyacinthoides non-scripta were due to different temperature requirements of the seeds and they suggested that the spring germinators act as insurance against loss of the over-wintering seedlings. There is no evidence for distinct seed morphs with respect to germination requirements in R. sceleratus (see Chapter 13) but the

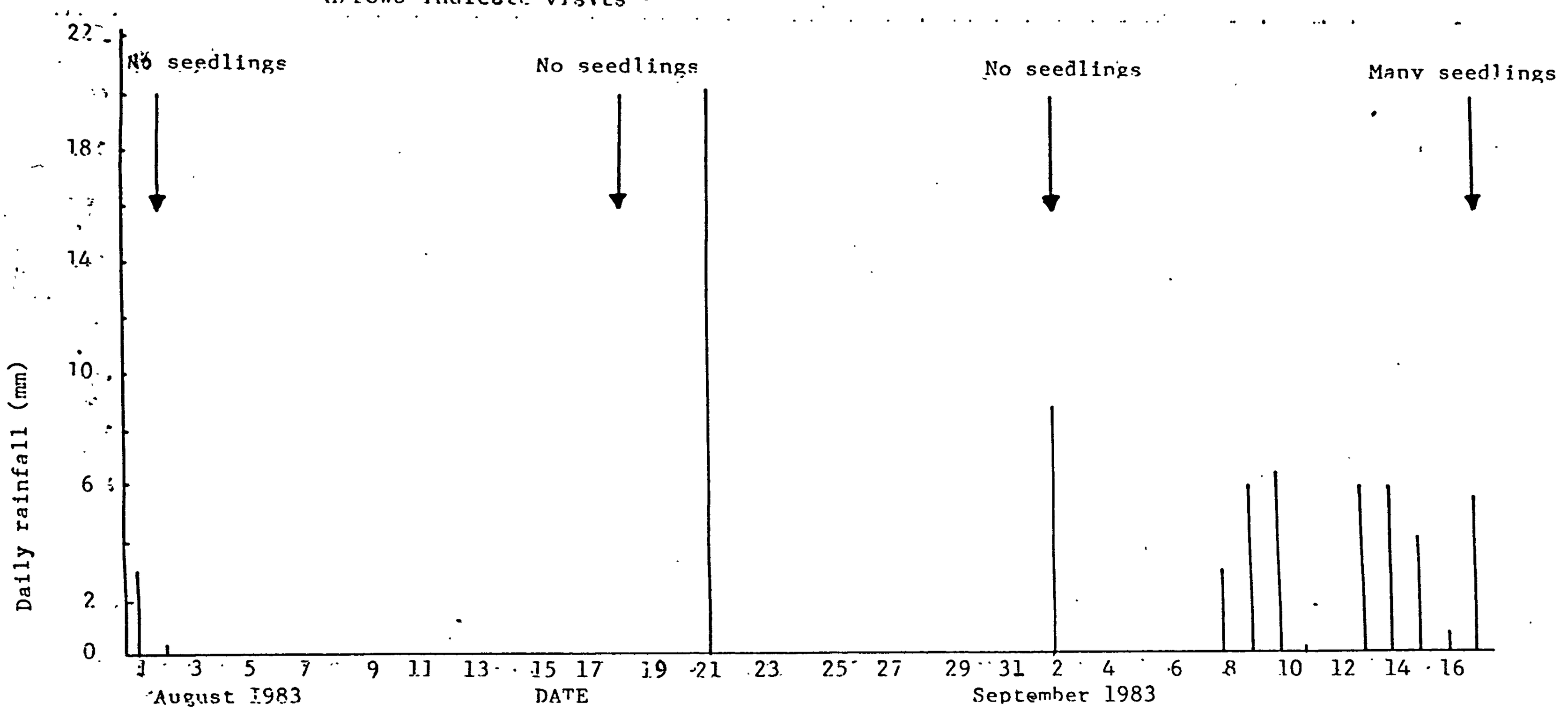


Figure 12.20

Daily rainfall from 1st August to 17th September 1983 (from Oxford Met. station, see Appendix 2) and the emergence of R. sceleratus during that period.

role of the spring germinating seedlings may be the same (see section 12.3.6).

12.3.3 Survivorship patterns

R. sceleratus shows a survivorship pattern of somewhere between Deevey Type 11 and Type 111. In terms of mortality this is somewhere between constant mortality with age and a decrease in risk of mortality with age. The Deevey Type 111 pattern appears to be typical of over-wintering cohorts whereas the Type 11 pattern is typical of later (Spring/Summer) cohorts.

This pattern is in marked contrast to the published survivorship patterns of many other annual plants. Survivorship curves for Vulpia membranacea (Watkinson, 1978a; 1978b; Watkinson and Harper, 1978), Cerastium atrovirens (Mack, 1976) and Phlox drummondii (Leverich and Levin, 1979) show a negatively skewed Deevey Type I survivorship curve, whereas annuals such as Lactuca serriola (Marks and Prince, 1981), Spergula vernalis (Symonides, 1977), Minuartia uniflora and Sedum smallii (Sharitz and McCormick, 1973), Salicornia europaea (Jefferies et al, 1981) show Deevey Type II or III survivorship patterns.

It has been suggested (Watkinson and Harper, 1978; Klemow and Raynal, 1983) that two groups of annuals can be recognised on survivorship pattern, fecundity and the survival of seed in the seed bank. One group has a Deevey Type I survivorship pattern, low fecundity and low survival of seed in the seed bank. The other group has a Deevey Type II or III survivorship pattern high fecundity and high seed survival in the seed bank.

Watkinson and Harper (1978) suggest that these characteristics are related to the predictability of the habitat. Plants in stable, predictable habitats are of the Deevey Type 1 group and plants from unstable, unpredictable habitats are of the Deevey Type 11/111 group.

This study showed yearly seed production figures for R. sceleratus of between 73 and 16,950 per plant; these are high relative to many annuals (Salisbury, 1942). Toorn (1980) records that 1m tall individuals of R. sceleratus can yield 500,000 seeds. This is many times the maximum for this species recorded by Salisbury (1942) of c. 30,000. This may be due to the 'optimal' conditions experienced by these plants growing on the newly drained Polders in the Netherlands.

With regard to seed survival in the seed bank, Toorn (1980) found that seeds were still viable after five years in the soil. As in this study, Thompson and Grime (1979) found that R. sceleratus has a seed bank and this was described as a '..fairly substantial persistent seed bank..' (K. Thompson pers. comm.).

On the basis of this study R. sceleratus would be placed in the Deevey Type II/III group as it shows all the features (Type II or III survivorship pattern, high fecundity and high seed survival in the soil) relevant to this group. It is also found in unpredictable habitats and so, following the suggestion of Watkinson and Harper (1978), this species would be expected to be in this group.

Cohen (1966) suggests that plants in unpredictable habitats should show good seed bank survival, high fecundity and a low percentage emergence of seeds from the seed bank. Regarding seed bank emergence, an estimated 80,000 seeds were produced during the 1983 season but only

about 1,500 seeds emerged before the start of the next seed production period. It is clear that a large number of these seeds would have been added to the seed bank.

12.3.4 Timing of Flowering

The general synchrony of flowering in both years supports the finding of Samarakoon and Horton (1981) that flowering is under photoperiodic control. They found that R. sceleratus was a Long Day plant requiring a 16 hour photoperiod for 5 days to obtain 100% flowering. There is, however, a trend towards later flowering of the later cohorts in both years and no flowering in very late cohorts (Tables 12.5 and 12.6).

Size (based on rosette diameter) could be a secondary controlling factor but some rosettes of all sizes (including those of <1 cm) flowered on the 20 June 1983. It has been suggested that the delay in flowering reported in Chapters 10 and 11 was related to size.

The short delay (1 visit) in the flowering of May 1983 emerging cohorts may reflect some age dependence and a minimum vegetative period of 5 weeks. This age dependence was also found in the later cohorts of 1984. Bakker et al (1966) found that autumn and spring emerging plants flowered in June but June emerging plants did not flower until August, suggesting a 4 to 8 week minimum vegetative period.

However, the June/July 1983 cohorts survived up to 8 weeks but did not flower (Table 12.5). This lack of flowering may be related to drought. More research is required to understand the control of flowering in this species.

12.3.5 Submergence

This study shows that submergence influences plant survival (Tables 12.9, 12.10, 12.11 and 12.12). Generally submergence results in increased mortality. Rosette diameter was found to be more strongly correlated with survival than rosette age. Survival was found to increase with increasing rosette diameter (Tables 12.10 and 12.12). The exception to this was the 'large rosettes' in the submergence period of 1983 which showed increased mortality compared to medium and small rosettes (Table 12.12). Rosettes of the size of the large rosettes (5 to 10cm) were not present in the submergence period of 1984 (maximum rosette diameter of 4cm). Whether or not this is a general rule will require further study. It is interesting to note that no mortality of seedlings was recorded during the one-week submergence treatments in the greenhouse (experiments 4, 5 and 6 - see section 2.4). Again further research is needed to understand the reasons for this difference between greenhouse and field results.

12.3.6 Life history tactics

In this study the main life history tactic (see Chapter 1) of R. sceleratus was that of a winter annual (i.e. emergence in autumn and flowering in late May/early June of the following year) (Harper, 1977). This is not the only tactic shown by these plants; a secondary one of a summer annual (emergence in April/May and flowering in June of the same year) is also shown at this site.

The major differences between the two main tactics (winter/summer

annuals) are in survival and fecundity. Overall the winter annuals had low survival but very high fecundity compared with the summer annuals which had relatively high survival but low fecundity (Table 12.14).

These two tactics can be compared using the measure of relative 'fitness' of survivorship x fecundity (Silvertown, 1982). These give 70 to 340 for autumn cohorts and 9 to 252 for spring cohorts. The interesting point here is that the improved survivorship in the spring cohorts almost compensates for the decreased fecundity.

This pattern of late germination (i.e. spring) favouring survival and early germination (i.e. autumn) favouring fecundity has been found in the annuals L. serriola (Marks and Prince, 1981) and V. membranacea (Watkinson, 1978a; 1978b; Watkinson and Harper, 1978). Law et al (1977) studying Poa annua found that delayed reproduction favoured increased fecundity due to increased growth.

R. sceleratus also shows a range of tactics from autumn to spring annual due to emergence between the two peaks. The initial large rosettes found in December 1982, as already discussed, would have germinated during the summer of 1982 and could be classed as "biennial" (or monocarpic perennial) (Table 12.15). This is supported by Salisbury (1970) who records R. sceleratus as showing either a "biennial" or an annual life history.

Bakker et al (1966) consider R. sceleratus to be an ephemeral plant (a life-cycle of less than 4 months). This is a rather limited classification for this multiple tactician and clearly not the case for many of the plants in this study. The ephemeral tactic not found in this study, but recorded by Bakker et al (1966) and Toorn (1980) is that

Table 12.14

The main life history tactics shown by R. sceleratus plants at the Port Meadow ditch site during 3/12/82 to 4/8/84.

Emergence date	Flowering date	Survivorship to flowering	Fecundity (per plant range)	"Tactic"
Autumn	May/June	0.01-0.02	7000-17000	winter annual
Spring	June/July	0.03-0.14	300-1800	summer annual

Table 12.15

The range of life history tactics shown by R. sceleratus plants based on the Port Meadow results and other named sources.

Emergence date	Flowering date	Survivorship to flowering	Fecundity	"Tactics"
Late summer	May/June	low	high	biennial[1]
Autumn	May/June	low	high	winter annual
Early winter	June	low?	high?	winter annual
Early spring	June	high	low	summer annual
Spring	June/July	high	low	summer annual
Early summer	August	low?	low?	ephemeral[2]

1 = see Salisbury (1970).
2 = see Bakker et al (1966) and Toorn (1980).
? = uncertain

of seedlings emerging in June and flowering in August (Table 12.15). The June/July emerging plants all died in this study. Bakker et al (1966) consider these plants as arising from freshly dropped seed.

12.4 Summary

1. R. sceleratus shows emergence peaks in autumn and spring, with the autumn the more important in terms of numbers.

2. Survivorship is between Deevey Type II and Deevey Type III in pattern. There is a tendency for earlier cohorts (autumn/winter) to show Deevey Type III and later cohorts (spring) to show the Deevey Type II pattern.

3. R. sceleratus plants show many of the features associated in other plants with these survivorship patterns, such as high fecundity and a seed bank.

4. Early cohorts (autumn) can show lower survival to flowering than later (spring) emerging cohorts. The seed output/plant of these earlier plants is, however, much greater. This is related to the large flowering stem produced by these well established plants.

5. Survival during submergence has been shown to be size, rather than age, dependent. Smaller plants have a greater risk of mortality.

Chapter 13

Germination of Ranunculus sceleratus Seeds

"Seed polymorphism .. enables a proportion of the population to avoid major hazards.."

(Harper, 1965:257)

13.1 Introduction

Many authors have commented upon the promotion of germination in Ranunculus sceleratus with diurnal fluctuating temperatures (e.g. Salisbury, 1942; Stiles, 1950; Koller, 1955; Mayer and Poljakoff-Mayber, 1975). Mayer and Poljakoff-Mayber (1975) state that promotion of germination in this species only occurs in the light. However, Salisbury (1942) comments upon a promotion of germination in the dark by diurnal fluctuating temperatures.

These results are the more confusing because they have the same original source, that of Gassner (1915), even though this is not cited by Mayer and Poljakoff-Mayber (1975). They cite Stiles (1950) (who cites Gassner (1915)) and Koller (1955) (who cites Stiles, 1950!). These conflicting results were dealt with by referring to the original source.

13.2 Case Study 1: Gassner (1915)

Gassner (1915) conducted several hundred separate germination

experiments, usually using 3 lots of 100 seeds in each case. His results represent work upon nearly 100,000 seeds, the largest work on R. sceleratus seeds known. The seeds were subjected to various treatments, such as constant or fluctuating temperatures. However, he made little attempt to systematise or summarise his data. His results are presented in tables with the means of each set of 3 seed lots and duplicate experiments are listed in different tables. The following is an attempt to systemise and summarise Gassner's results.

Gassner's experiments on alternating temperatures are complicated by the fact that two different alternating temperature regimes are mixed throughout his results. The basic pattern was a period of 4 hours at one temperature followed by a period of 20 hours at another. However, an experiment involving a single pair of fluctuating temperatures was performed in two ways, either a 4 hour period at the higher temperature followed by 20 hours at the lower one ("High-Low") or 4 hours at the lower one followed by 20 hours at the higher one ("Low-High").

When these experiments were conducted in the dark, only the relative lengths of the high and low temperature periods were being altered. However, when he conducted the experiments in the light, the light period was always given along with the high temperature period. In the latter experiments two variables were changed, that of the relative lengths of the high and low temperature periods and the length of the light period (Table 13.1).

Various pairs of alternating temperatures were used, although four predominate, these were:

12-28°C; 19-28°C; 6-19°C; 12-19°C.

Table 13.1

The environmental conditions used by Gassner (1915) for experiments on the germination of R. sceleratus seeds.

	Temperature regime	Photoperiod
(a)	4 hours high + 20 hours low	4 hours**
(b)	4 hours low + 20 hours high	20 hours**
(c)	4 hours high + 20 hours low	none
(d)	4 hours low + 20 hours high	none

** with high temperature

Experiments were also conducted at constant temperatures in the light and dark with very little germination in either case. Germination never exceeded 1% and this result was independent of the temperature used, whether 33°C, 28°C, 24°C, 19°C, 12°C or 6°C. The photoperiod used in these experiments in the light is not given and so either they were conducted under constant light or a combination of the 20 hours/4 hours used in the other experiments. The photoperiod is stated for all other experiments.

In order to look closely at the response of R. sceleratus to diurnal alternations of temperature, percentage germination will be plotted against the temperature fluctuation (i.e. high temperature minus low temperature). This method was used by Thompson and Grime (1983) for a similar study.

The High-Low treatment in the light (Figure 13.1) shows:

1. Promotion of germination by alternating temperatures in the light,

2. Increased fluctuations in temperature increase promotion,

3. The amount of promotion is independent of the upper temperature.

The Low-High treatment in the light (Figure 13.1) shows a similar result but the promotion of germination is less. Gassner suggests that the reduced promotion in this treatment is due to the long period at high temperature inhibiting germination. There is some evidence that the absolute temperatures are affecting germination as one point does not fit in the general pattern.

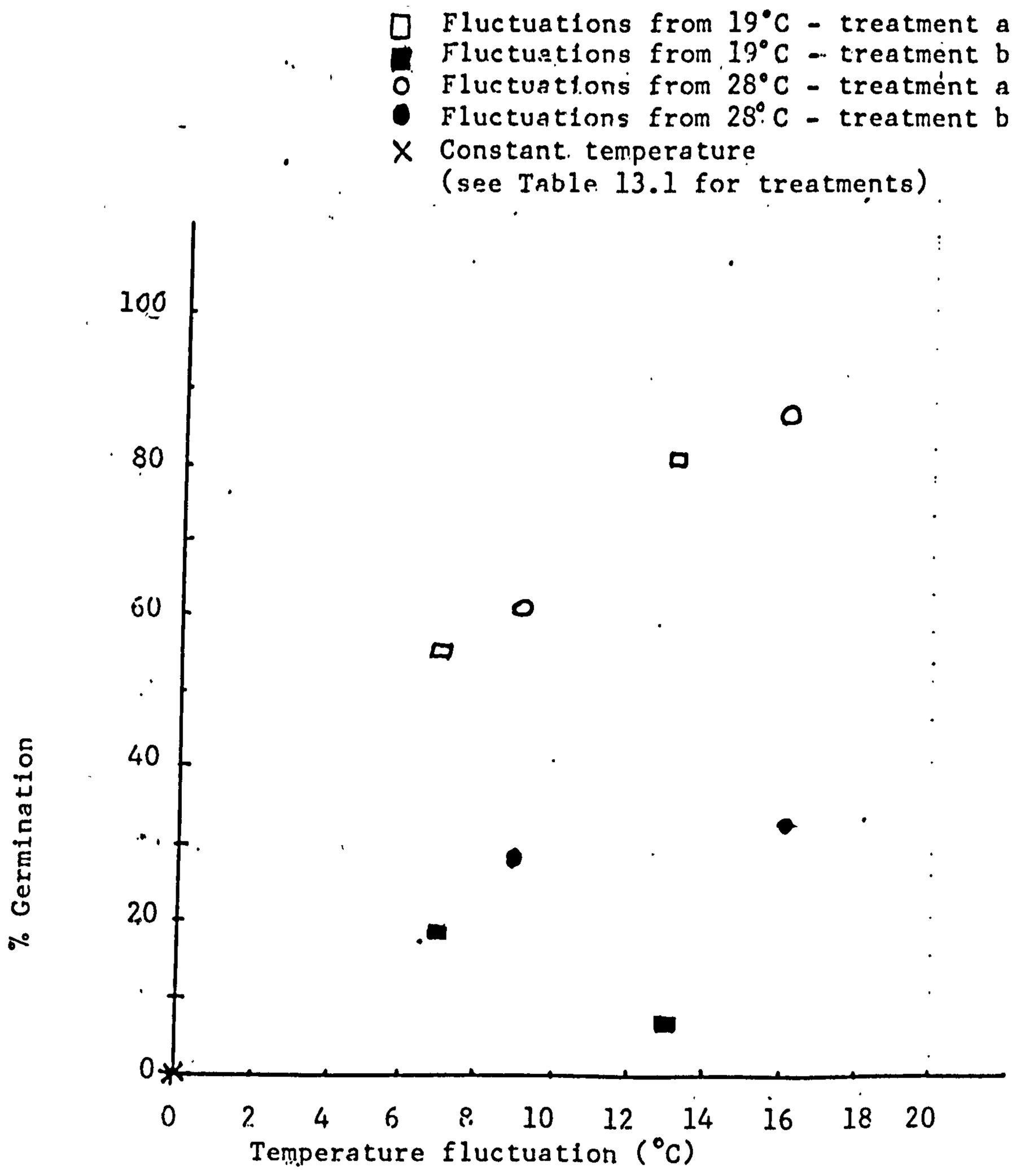


Figure 13.1

Percentage germination of R. sceleratus seeds in the light against diurnal fluctuation in temperature (see text for treatments; data from Gassner, 1915).

The High-Low treatment in the dark (Figure 13.2) also shows promotion of germination and increased promotion with increased temperature fluctuations but not as great as with a light period. The Low-High treatment in the dark (Figure 13.2) shows virtually no change in germination from constant temperatures with little or no germination (never exceeding 4%).

The overall conclusions from Gassner's work are:

1. There was virtually no germination at constant temperatures in the light or dark, independent of absolute temperature.

2. Diurnal fluctuations in temperature promote germination in the light or dark, but the promotion is greater in the light. The greater the fluctuation the greater the promotion in germination.

3. Long periods at high temperature (or short periods at low temperature) inhibit (to some extent) this promotion of germination in both the light and dark.

This finding of germination promotion by alternating temperatures in the dark is suprising since Stiles (1950), cited later by Koller (1955) and Mayer and Poljakoff-Mayber (1975), states that this was not the case - based on Gassner's work! The complex and confusing nature of Gassner's results and the fact that it was written in German may have lead to this error.

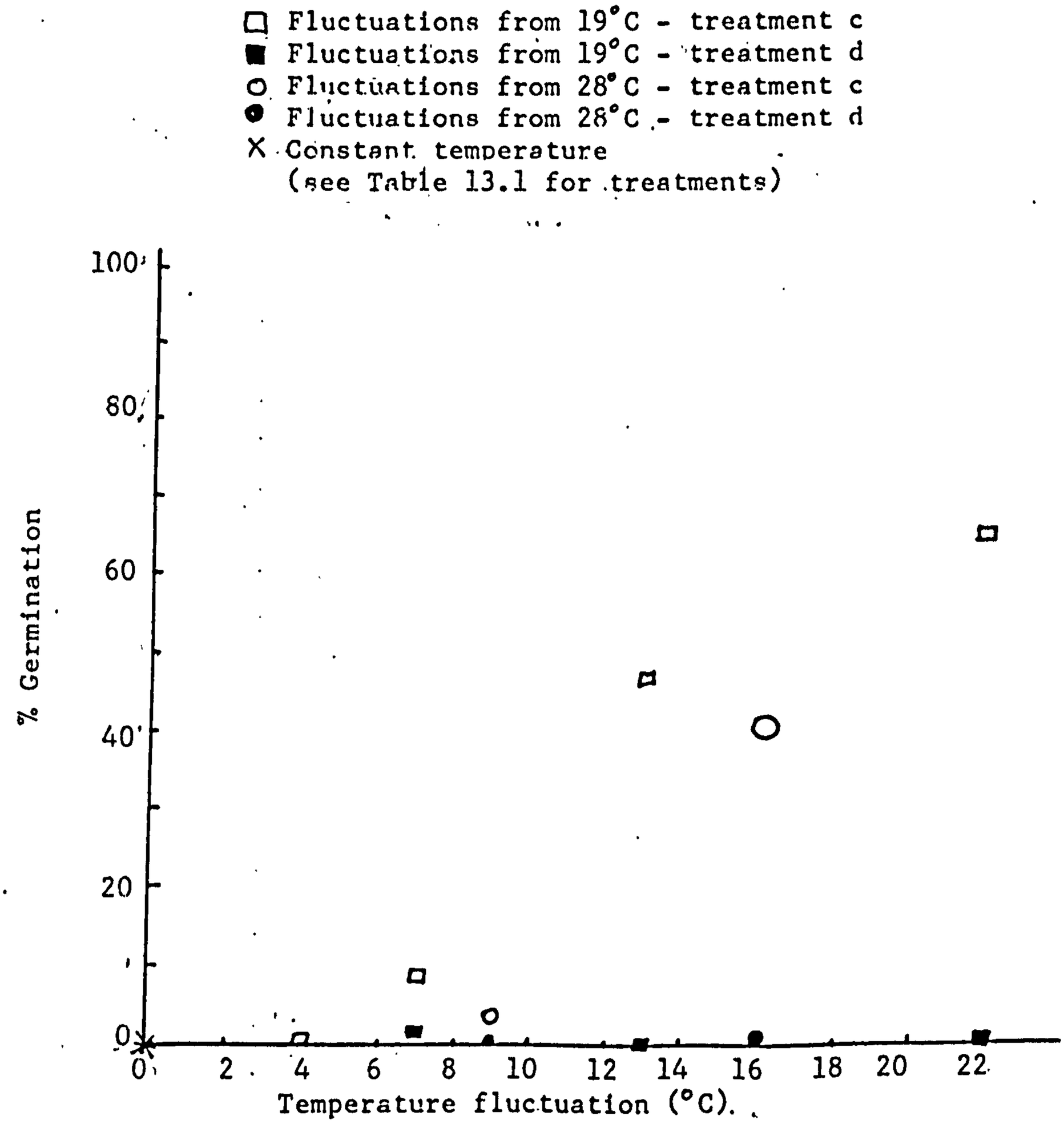


Figure 13.2

Percentage germination of R. sceleratus seeds in the dark against diurnal fluctuations in temperature (see text for treatments; data from Gassner, 1915).

13.3 Case Study 2: Toorn and Hove (1976; 1982)

Toorn and Hove (1976; 1982) carried out germination experiments on R. sceleratus on a much smaller scale than Gassner (1915). The pairs of diurnal fluctuating temperatures used all had a lower temperature of 5°C. The following pairs of temperatures were used:

5-5 (constant)°C; 5-10°C; 5-15°C; 5-20°C; 5-25°C; 5-30°C.

The percentage germination obtained is plotted against the temperature fluctuation (Figure 13.3). It can be argued that the graph shows promotion of germination by alternating temperatures, but the fall off in germination for the 5-10°C fluctuations may be due to the absolute temperatures being sub-optimal for germination. Mayer and Poljakoff-Mayber (1975) in a review of this subject suggest that the absolute temperatures are of secondary importance provided they are in a range in which the seeds can germinate and viability is not affected.

Grime et al (1981) found that a 5°C fluctuation using absolute temperatures of 15 and 20°C gave 83% germination in R. sceleratus. However, these seeds were not freshly collected and Toorn and Hove went on to show that with soil storage at ambient temperature or dry storage at 5°C seeds would eventually germinate very well at 5-10°C fluctuations and even at a constant 5°C (Figure 13.3). Toorn and Hove consider this as an example of stratification (a low-temperature requirement for germination (see Mayer and Poljakoff-Mayber, 1975) but although the seeds did not germinate well at 5-10°C they did at 5-15°C. Therefore this is not an example of stratification.

There are two possible explanations for the increased germination at 5-

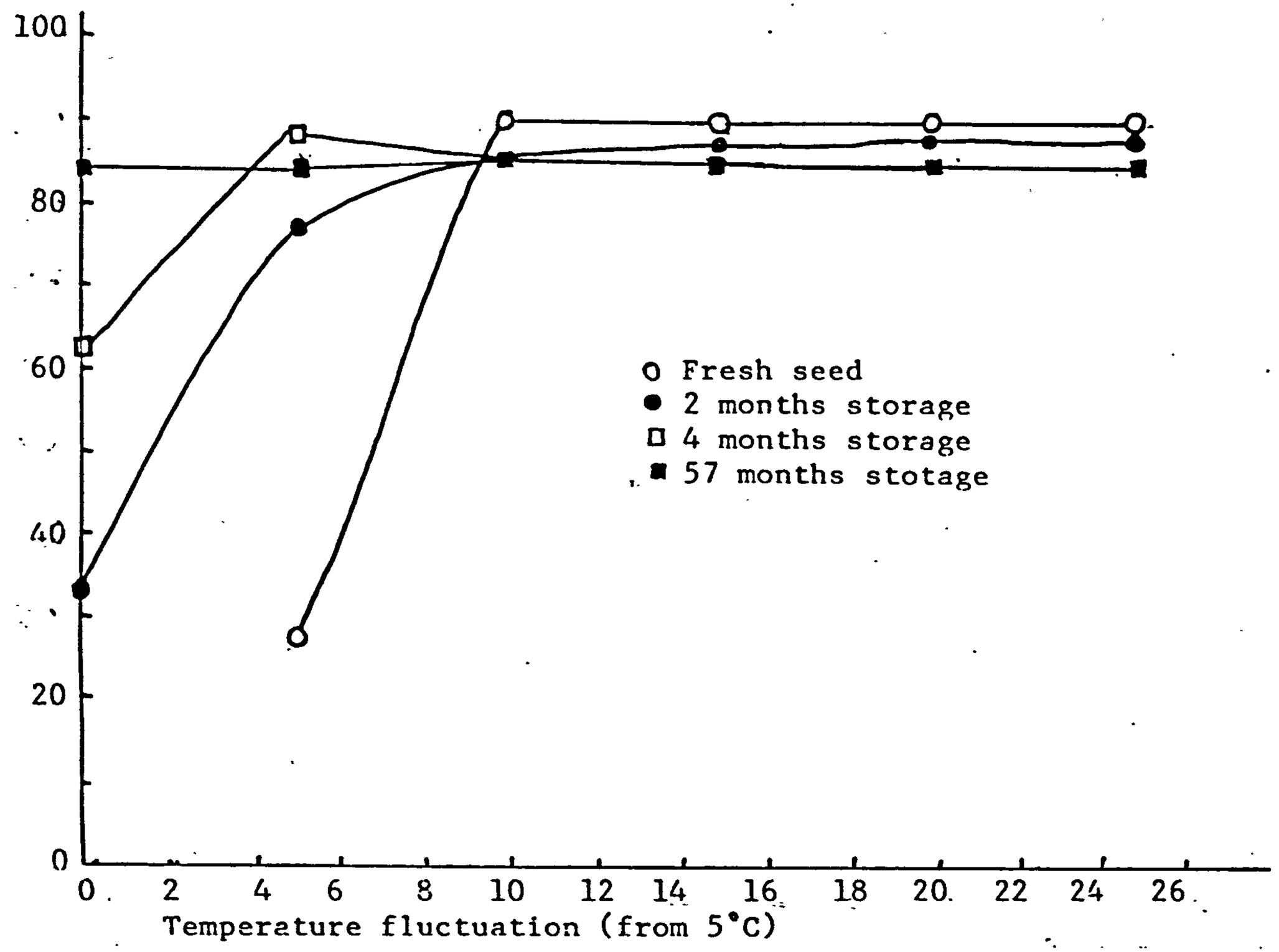


Figure 13.3

Percentage germination of R. sceleratus seed in the light against diurnal fluctuations in temperature at various times of storage (at 5°C) (data from Toorn and Hove, 1976 and 1982).

5°C and 5-10°C following storage. Firstly, that the fresh seeds are unable to germinate because of the low temperatures but germination is possible after storage due to internal changes in the seed. A second explanation is that there was insufficient temperature fluctuation to promote germination but later germination was possible due to loss of the requirement of alternating temperatures to germinate. The latter effect of a gradual loss of the need for temperature fluctuation requirement for germination has been found by Thompson and Grime (1983) with seeds of Carex otrubae and Sieglingia decumbens.

The gradual loss of temperature fluctuation requirement is also evident in the results of Gassner (1915) working with R. sceleratus (Figure 13.4) and Whitehead (1971) refers to unpublished research that found the need for fluctuating temperatures in R. sceleratus gradually declined until after 6 or 7 years the requirement had been totally lost (unfortunately the data from these experiments have not been traced). Hence the latter explanation is very plausible.

13.4 Other germination results

Lehmann (1911) conducted some germination experiments under uncontrolled conditions and so his results are of little value. He obtained between 37 and 52% germination in the light and no germination in the dark. Grime et al (1981,) as already quoted, found 83% germination with 15°C (dark)-20°C (light) in the light (18 hour photoperiod) but under the same temperature conditions in the dark no germination occurred. Whitehead (1971) refers to unpublished work where 97% germination occurred with diurnal fluctuations of 8-10°C. He goes on to state that maximum germination was achieved with a night minimum temperature of

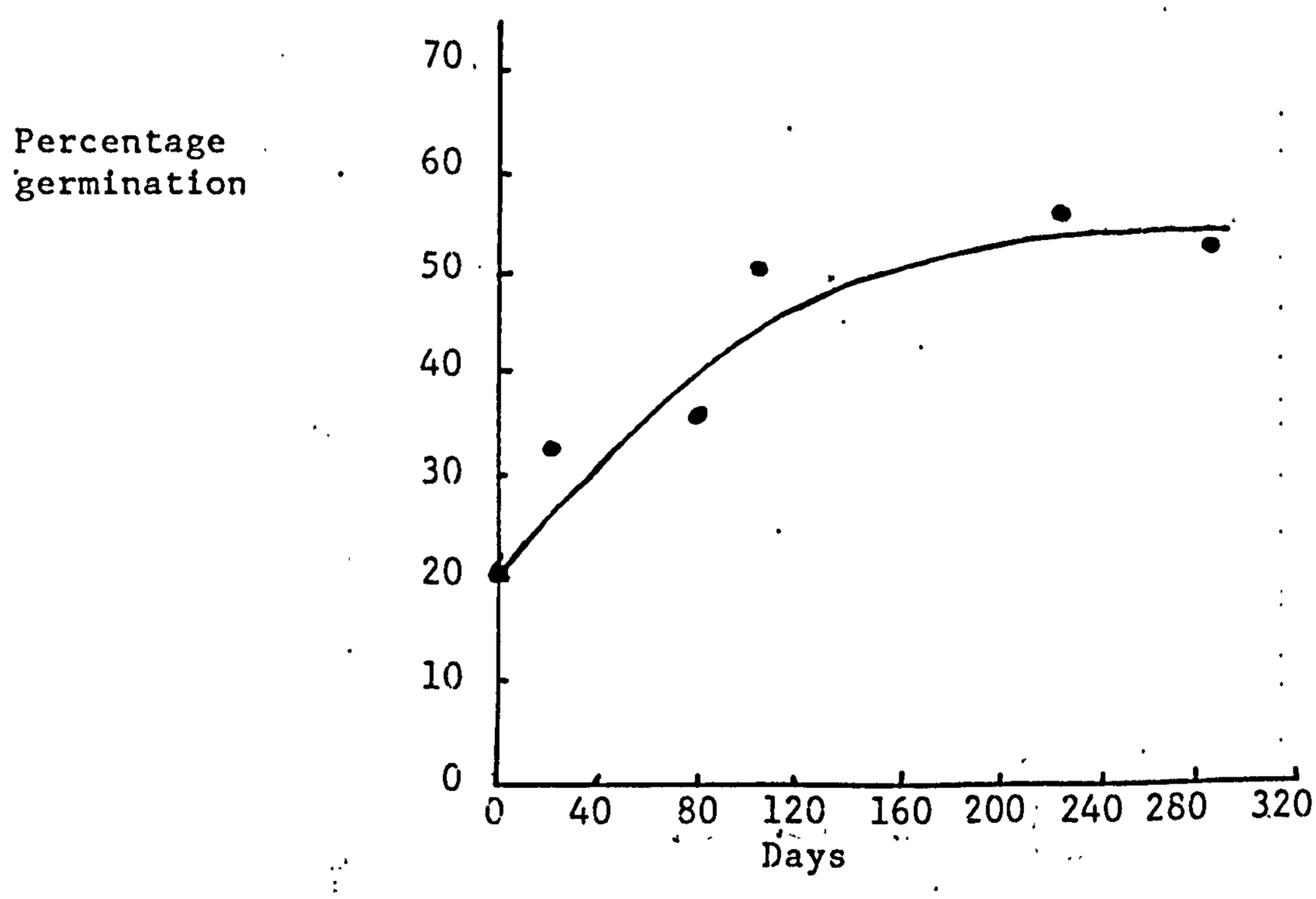


Figure 13.4

Percentage germination of R. sceleratus seed with time under dark conditions and 16°C diurnal fluctuations in temperature (4 hours at 12°C and 20 hours at 28°C; data from Gassner, 1915).

5°C. These results are similar to those of Toorn and Hove (1976; 1982) (Figure 13.3).

13.5 Experimental results

Germination trials were carried out on the seeds of R. sceleratus at 20-20°C and 15°C (dark)-25°C (light) in the light (18 hour photoperiod) (see section 2.4 under experiment 9). The constant temperature treatment gave 18% germination whereas the 10°C diurnal fluctuation gave 61% germination. The high germination for the constant temperature probably resulted because the seeds were three months old and had been in dry storage at about 5°C (see Figure 13.3). There is a clear promotion of germination with fluctuating temperatures in the light.

The ability of R. sceleratus seeds to germinate underwater was studied in a greenhouse experiment (see section 2.4 under experiment 8). Germination of seeds under 8cm of water was 32% compared to a control germination in air of 89%. The submerged seeds experienced reduced temperature fluctuations compared to controls. The average diurnal fluctuation of air temperature for controls was 24.1°C whereas the water temperature showed an average diurnal fluctuation of 11.4°C. Although the amount of germination differed considerably, patterns of germination (Figure 13.5) were very similar, the main difference being a six day delay in the submerged seeds.

13.6 Discussion

The above results show that germination of R. sceleratus seeds can be

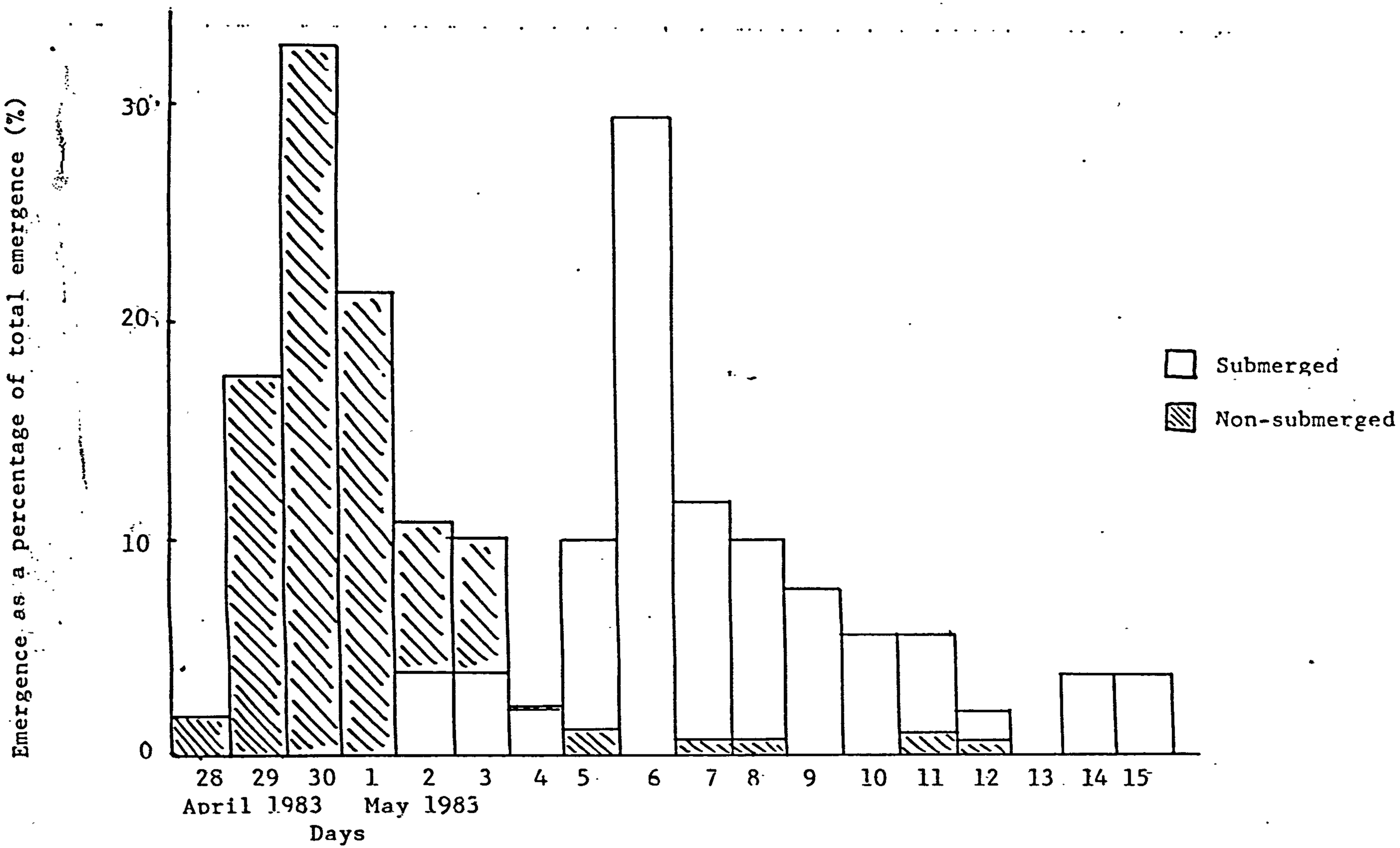


Figure 13.5

The distribution of R. sceleratus seed emergence with time for submerged and non-submerged conditions with time plotted as a percentage of total emergence.

promoted by diurnal fluctuating temperatures both in the light and dark, and the promotion is less in the light. Absolute temperatures, the period of exposure to these temperatures and seed age have a considerable effect on germination.

The promotion of germination in the light by alternating temperatures is a common feature of many wetland plants (Thompson et al, 1977; Thompson and Grime, 1983). It has been suggested that this has evolved because it enables the seeds to germinate when the fall in water level occurs in spring (Thompson and Grime, 1983). This also coincides with the beginning of the period most favourable for growth.

However, germination in this species also occurs in the Autumn which is preceded by a period of unfavourable conditions. The greater fecundity of the surviving autumn plants (see Chapter 12) suggests that this is an alternative strategy from Spring germination which favours survival rather than fecundity (see Chapter 12).

Another feature common to wetland plants is the lack of dark germination. It has been suggested to have evolved because of the low survival probability of seedlings germinating in deep water (Mayer and Poljakoff-Mayber, 1975). It will also prevent germination below a plant canopy, an important point considering that many mud colonisers (like R. sceleratus) are poor competitors (Salisbury, 1970). Dark germination in response to large temperature fluctuations will result in germination of slightly buried seeds after the water level has gone down or covering vegetation has been removed by disturbance.

Thompson and Grime (1983) found that the requirement of temperature fluctuations to stimulate germination in the dark is a common feature of

many wetland plant seeds. They found that in general a greater fluctuation in temperature was required to bring about 50% germination in the dark than in the light. This is consistent with the findings of Gassner (1915) reported here.

The evolution of germination responses that match changes in the environment are not suprising when germination date and fecundity are considered (Cook, 1980; Baskin and Baskin, 1972). These results show that small differences in germination date can result in major differences in reproductive output. The work of Thompson (1975) reflects the matching of environment with germination in populations of Silene dioica. Toorn and Hove (1976) state that R. sceleratus seed sown (and emerging) after June failed to produce seed. The importance of emergence date and seed production in this species is clear from the field data collected in this study (Chapter 12).

Clearly the seeds of R. sceleratus can germinate underwater. This ability is shown by other wetland plants, e.g. Typha latifolia (Weller, 1975); Phragmites communis (Spence, 1983) and Nasturtium officinale (Morinaga, 1926a). However, Morinaga (1926a; 1926b) found that many non-wetland plants can germinate underwater and concluded that in general small seeds are able to germinate underwater, independent of phylogeny.

Salisbury (1942;1974) has shown a link between seed size and habitat (smaller seeds are found in species of disturbed or open areas) and so there is perhaps a link between habitat and the ability to germinate underwater. Morinaga (1926a) also found that boiling the water used in the experiments often reduced underwater germination. He concluded that oxygen levels are important in the control of underwater germination.

In general, reduction in oxygen from atmospheric levels results in reduced germination (Mayer and Poljakoff-Mayber, 1975). However, Morinaga (1926c) and Sifton (1959) found that Typha latifolia seeds germinate better under reduced oxygen levels and this species germinates better underwater than in air (Morinaga, 1926b; Weller, 1975). This suggests that the germination of seeds underwater can be related to the response of seeds to oxygen levels.

The reduction of germination in R. sceleratus underwater could be related to reduced oxygen levels. Temperature fluctuations were also reduced and this may also have resulted in a reduction in germination. This is not likely to be the full explanation as temperature fluctuations of around 11°C would, based on the literature cited, have given much greater germination.

From the above discussion it can be seen that seeds of R. sceleratus are polymorphic with respect to fluctuating temperature requirements. A small proportion show either no innate dormancy or innate dormancy that is quickly lost, whereas the remaining seeds require differing diurnal fluctuations in temperature to break innate dormancy. Harper (1965) points out that germination polymorphism allows a proportion of the population to avoid a major hazard. Considering the low survival probability of young seedlings when submerged (Chapter 12), it is not suprising that R. sceleratus has evolved germination polymorphism.

The polymorphic germination of R. sceleratus results in a small "background" germination taking place whenever moisture is available and temperatures are high enough, and peaks in germination whenever fluctuating temperatures occur. There may also be peaks following disturbance and a fall in water level, depending on time of year. This.

allows R. sceleratus to spread germination throughout the year, but with a concentration at the times most favourable to growth and/or fecundity.

13.7 Summary

1. R. sceleratus seeds show promotion of germination in the light and dark with diurnal fluctuations in temperature. The promotion is greater in the light.

2. R. sceleratus seeds are able to emerge underwater but the percentage is lower than for emergence in air.

3. The polymorphic nature of germination in R. sceleratus can be related to the unpredictability of its habitat.

Chapter 14

Future Work and Conclusions

"Ecological patterns, about which we construct theories, are only interesting if they are repeated"

(MacArthur, 1968)

14.1 Future work

With hindsight, it is clear that fewer topics should have been studied so that each topic could have been studied in greater depth. Because a large range of topics were investigated many of these deserve further research. For example, the promotion of germination in R. sceleratus seeds with fluctuating temperatures could be investigated using a thermo-gradient bar which allows a large range of temperature-pairs to be investigated at once (Grime and Thompson, 1976; Thompson and Grime, 1983). Also the relationship between the two Port Meadow site populations could be investigated further with inter-site ramet transplants. The following are topics with scope for future study.

14.1.1 Novel methodology for dry weight allocation studies

In section 2.6 a graphical technique for the measurement of dry weight allocation was proposed. However, this thesis has shed some light on the problems as well as benefits of the methodology. The benefits were discussed in section 2.6 and were mainly associated with the removal of

plant size effects without the introduction of error due to the y-axis intercept. Two major problems have arisen. Firstly, with the R. sceleratus data the range of total dry weights was such that a 'slope allocation' could not be properly assessed (Chapter 10). Secondly, the lack of flowering R. repens plants in the transplant garden (Chapter 5) again made the 'slope allocation' difficult to measure accurately. These problems are probably least likely to hamper field allocation studies and most likely to hamper experiments under controlled conditions. This may be a very useful tool in the comparative study of different field populations in terms of allocation pattern. Further research is required to see how generally the methodology can be applied.

14.1.2 Classification of clonal perennial strategies

Several authors have recognised differing clonal perennial strategies and some have proposed classifications. Most of these are based on growth form but one is based on demography, growth rates and allocation (Schmid, 1984). Hartnett and Bazzaz (1985b) used a classification based on "territorial" strategies similar to the "phalanx-guerilla" strategies proposed by Lovett Doust (1981a) and Harper (1981). The latter is used widely in the literature (e.g. Bulow-Olsen et al, 1983; Dickerman and Wetzel, 1985; Schmid and Harper, 1985).

A traditional description of clonal perennials as stoloniferous or rhizomatous (e.g. Clapham et al, 1962) [or both (Douglas, 1981)] classifies according to gross morphology. Discussions of clonal perennials often compare these different types without reference to the morphological differences between them (e.g. Hartnett and Bazzaz,

1985b). It may be that they can be considered as above ground and below ground solutions of a similar problem or that fundamental differences arise due the different nature of stolons and rhizomes. This could prove an interesting study for future work. A particularly interesting study would be the balance between allocation to stolons and rhizomes in plants that produced both structures (e.g. Mimulus primuloides; Douglas, 1981). This study might shed light on functional and strategic differences between the two structures.

14.1.3 Seed ecology of R. sceleratus

R. sceleratus plants have been shown to be very plastic in terms of mean seed weight (0.08-0.25mg), height of flowering stem (5-120cm), seed output/plant (30-500,000 seeds) and the number of seeds/seed head (25-335 seeds) (Chapters 10 to 13). These findings raise interesting questions about the seed ecology of this species that would be of interest for future work.

For example;

- the effects of seed size on germination, establishment and seed output.
- the control of the number of seeds/seed head which is extremely variable in this species.
- the influence of the height of flowering stem on seed dispersal and seed output.

14.2 Conclusions

14.2.1 *Ranunculus repens*

One of the aims of this project was to study the tactical changes in dry weight allocation in relation to submergence in the perennial *R. repens*. The submegence experiments (Chapter 3) showed that there was an increase in dry weight allocation in the short term to underground structures in the submerged plants compared to the controls, both in absolute terms and relative to above ground allocation (i.e. increased root:shoot ratios). These findings are consistent with other research upon plants in 'stressful' environments (Fitter and Hay, 1981) but in this case it did not involve an increase in allocation to subterranean storage organs. It is suggested that the increased emphasis on underground allocation may be related to nutrient deficiency (Bradshaw *et al*, 1964).

In the longer term experiment (Chapter 5) the tactical changes in allocation to underground structures varied with the site of origin of the plants. The Port Meadow submerged site plants showed an increase in 'root:shoot' ratio with the submergence treatment whereas the Port Meadow non-submerged site plants showed a decrease and the Open University plants showed no change. This result suggests that the three *R. repens* site populations are genetically distinct. This conclusion is supported by other differences in tactical allocation pattern (Chapter 5), in growth form (Chapter 7) and dry weight per unit length of stolons (Chapter 8).

However, despite the differences in tactial allocation pattern in both the short term and the long term submergence experiments dry weight allocation to stolons was always maintained or increased and this was

independent of site of origin (Table 14.1). This emphasis on stolon allocation is probably a reflection of the importance of stolons in the maintenance of population growth and colonisation in this species (Sarukhan and Gadgil, 1974).

One of the aims of this project was to look for genetic differeniation between populations of R. repens growing under different submergence regimes. There is considerable evidence for differentiation between the three populations studied but this is not necessarily related to submergence. The two Port Meadow populations have similarities in their patterns of tactical differences with respect to vegetative reproduction (Table 14.1). The similarity of the two populations is not suprising considering that it is probable that the Port Meadow non-submerged site plants originated from the Port Meadow submerged site plants (see Appendix 1).

The Open University site plants show a very different pattern of tactical differences between the submerged and control treatments compared to the Port Meadow plants (e.g. Table 14.1). A major distinction is the difference in stolon internode lengths between submerged and control treatments (Table 7.3). As discussed in Chapter 7 Lovett Doust (1981a) and Harper (1981) consider these to be important descriptors of clonal plant growth form. All three populations can be separated on the absolute changes, but only the Open University site plants had shorter stolon internode lengths in the submerged treatment relative to the control. Thus this research has not only shown that R. repens plants have considerable plasticity in growth form but also that this plasticity varies from population to population.

Lovett Doust (1981a) considered that the more guerilla-like strategy

Table 14.1

A review of the tactical differences in some vegetative reproductive traits resulting from a submergence treatment in R. repens. Short term differences are over c.3 months and long term over c.6 months (further details in Chapters 3, 5, 7 and 8).

Trait	Term	Site		
		Port Meadow submerged	Port Meadow non-submerged	Open University
Stolon allocation	short term	n/a	n/a	no difference
	long term	greater**	greater	no difference
Total stolon length	short term	n/a	n/a	lesser
	long term	greater	no difference	no difference
Stolon internode length	short term	n/a	n/a	n/a
	long term	greater	greater	lesser
Dry weight/mm stolon length	short term	n/a	n/a	lesser
	long term	lesser	lesser	no difference
Stolon:ramet allocation ratio	short term	n/a	n/a	lesser
	long term	greater	greater	no difference

** all differences are significant at $p<0.05$.
n/a = no information available.

shown by the R. repens plants in a woodland was related to the increased probability of a plant sampling a sunfleck, that is, it increases the probability of a more favourable light climate. This is similar to the argument of Ginzo and Lovell (1973a; 1973b) for the so-called 'getting away' strategy of tactical differences between R. repens plants on high and low nitrogen levels. They suggest that the production of fewer, longer stolons, containing less dry weight per cm of stolon length, would result in an increased probability of ramets being placed away from the unfavourable (low nitrogen) parent rosette.

It can be argued that Ginzo and Lovell's 'getting away' strategy is another description of a more guerilla-like growth form strategy. This increases habitat surveillance and increases the probability of a ramet's placement in a favourable site. Hartnett and Bazzaz (1983) explain the production of fewer, longer rhizomes by Solidago canadensis ramets once severed from their parents in similar terms; that is, the placement of future ramets away from the unfavourable parent site.

In contrast, however, the Open University site plants showed a more phalanx-like growth form in the submerged treatment than in control treatment in the transplant garden (Table 14.1). How can this be explained in the light of the previous discussion? The phalanx strategy is one of consolidation and slow radial spread. Perhaps this strategy has developed in response to the regular mowing of this site? Norris and Thomas (1983) have shown with Dactylis glomerata that different cutting regimes can result in genetic differentiation of populations.

The changes in dry weight per unit length of stolons were interpreted as being part of the 'getting away' strategy but these changes raise an interesting question. Why do the control treatment plants invest more

dry weight into stolons than the submergence treatment plants? It is likely that there are 'costs' to the reduction in dry weight per unit length of stolons that balance the 'benefits'. Further research into the functional significance of reduced dry weight per unit length is required.

Another aim of this project was to study the flowering behaviour of R. repens in relation to submergence. The results show that submergence results in both a reduction in the probability of a plant flowering and a reduction in number of flowers per flowering plant. These reductions are related to changes in the relationship between the probability of flowering and the number of flowers per flowering plant with total dry weight and ramet density in the submergence treatment plants.

14.2.2 R. sceleratus

The results for R. sceleratus show that this species has an opportunistic life history strategy (Harper, 1977) (Chapters 10 to 13). The demography results, together with the work of Bakker et al (1966) and Salisbury (1970), show that this species can exhibit the whole spectrum of life history tactics from ephemeral to "biennial", depending on germination date. The need for this spread of germination and tactics was clearly demonstrated by the Port Meadow population, which although showing the main tactic of winter annual, were dependent on summer annual plants as insurance against complete loss of the overwintering population.

Salisbury (1970) considers this species to be a specialist mud coloniser. He suggests that the ability of "seeds" to float for long

periods, the reduced germination in the dark compared to in the light, the involvement of alternating temperature in germination, the very high seed output and its extremely plastic form to be indicative of this specialism.

This study has (perhaps) revealed another part of this specialism. The submerged plants grown on the higher nutrient John Innes No. 3 (JI3) compost lacked the dry weight and dry weight allocation differences with submergence that were found with those grown in the JI1 and JI2 grown plants (Chapter 10). This may explain the association of this species with habitats subject to submergence and nutrient rich conditions (Fitter, 1978). Further research is needed to understand more fully this response to nutrients and submergence.

Although dry weight allocation differences were lost with higher nutrient levels, 'floral' (e.g. height of flowering stem, number of seed heads) differences were not lost (Chapter 10). This can be explained in terms of structural changes in the flowering stem, resulting from submergence, that took place before the higher nutrient level affected growth. These structural changes involved (or resulted in) a reduction in the branching of the flowering stem and led, because flowers tend to be borne terminally, to a reduction in number of seed heads/plant. This plasticity of form may be another specialism for this opportunistic primary colonist which may experience drought, submergence and other extremes. For example Salisbury (1970) reports full grown individuals with 5cm tall flowering stems growing on river ballast. This plasticity in form was apparent with the variation in height of the flowering stem in the Port Meadow population which allowed recently germinated plants to produce a small quantity of seed.

A further level of 'floral' plasticity is the ability to alter the number of seeds/seed head. This allowed the submerged plants in experiment 4 (Chapter 10) to show less reduction in seeds/plants than seed heads/plant. Cook (1976) has shown that another primary colonist Chenopodium rubrum also shows plasticity in the number of seeds/seed head. R. sceleratus plants also show considerable plasticity in individual seed weight but this variability appears not to be within a plant, population or between treatments grown at the same time but between different populations and treatments grown at different times. Further research is needed to understand this phenomenon (see section 14.1.3). Bradshaw (1965) suggests that phenotypic plasticity in growth may be a critical life history trait for plant persistence in temporally variable habitats.

14.2.3 Comparisons between the two Ranunculus species

The two species show contrasting effects of seasonal submergence on flowering. Submergence of R. repens plants tended to decrease the probability of flowering and the number of flowers, and reduce fecundity (Chapter 6), whereas R. sceleratus plants show no change in the probability of flowering (under greenhouse conditions), some reduction in the number of flowers but some compensation of this by an increase in the number of seeds/seed head (Chapter 10).

To compare sexual reproductive allocation on the same basis the R. repens results need to be converted to percentages (Table 14.2). Plants from all three populations show less percentage allocation to sexual reproductive structures with submergence. To compare this with R. sceleratus the allocation to receptacles needs to be added to the

Table 14.2

Dry weight of floral structures as a percentage of total dry weight (%, mean per plant) in pot grown R. repens plants. Plants were collected from the three field sites in January 1983 and subject to a submergence or control treatment and then harvested in August 1983 (n= 10; experiment 3).

Treatment	Site		
	Port Meadow submerged	Port Meadow non-submerged	Open University
Controls	0.251^{c**}	0.318^{d}	0.478^{e}
Submergence	0.064^{a}	0.166^{b}	0.053^{a}

Pooled S.E. = 0.052.
Anova: Site n.s.; Treatment $p<0.001$; Interaction $p<0.025$.
** different superscript means significantly different at $p<0.05$ using pooled S.E. in t-test (see Mead and Curnow, 1983).

Table 14.3

The dry weight of seeds plus receptacles as a percentage of total dry weight in R. sceleratus plants in experiment 4 (n= 5).

Treatment	John Innes number		
	1	2	3
Control	30.7^{c**}	32.3^{c}	29.1^{b}
Submergence	26.9^{a}	32.0^{c}	28.6^{b}

Pooled S.E. = 0.456.
Anova: Treatment $p<0.001$; John Innes no. $p<0.001$; Interaction $p<0.01$.
** different superscript means significantly different at $p<0.05$ using pooled S.E. in t-test (see Mead and Curnow, 1983).

Table 14.4

The dry weight of seeds plus receptacles plus flowering stems as a percentage of total dry weight in R. sceleratus plants in experiment 4 (n= 5).

Treatment	John Innes number		
	1	2	3
Control	75.0^{d**}	80.1^{e}	65.5^{ab}
Submergence	63.1^{a}	68.7^{c}	66.2^{bc}

Pooled S.E. = 0.966.
Anova: Treatment $p<0.001$; John Innes no. $p<0.001$; Interaction $p<0.001$.
** different superscript means significantly different at $p<0.05$ using pooled S.E. in t-test (see Mead and Curnow, 1983).

allocation to seeds (Table 14.3). Theoretically the dry weight allocation to flowering stem could also considered as sexual reproductive allocation (Thompson and Stewart, 1981). This is, however, not common practice (see Chapter 2) but some studies have included flowering stems in assessments of sexual reproductive allocation (Waite and Hutchings, 1982; Hawthorn and Cavers, 1978) (Table 14.4). Although submergence can result in reduced sexual reproductive allocation, for example, with JI1 grown R. sceleratus plants (Tables 14.3 & 14.4), the reduction in not as dramatic as with the R. repens (Table 14.2).

There is a very large difference in the comparative dry weight allocation to sexual reproduction allocation. The R. sceleratus plants have about 30% of their dry weight devoted to sexual reproduction excluding allocation to flowering stem and 60-80% including allocation to flowering stem. This compares with an dry weight allocation to sexual reproduction of <1% for R. repens plants. This difference reflects the relative importance of sexual reproduction for survival in annual and perennial plants. Sarukhan and Gadgil (1973) found that the modelled population growth of R. repens was not very sensitive to changes in sexual reproductive success but very sensitive to changes in ramet production, whereas failure of an annual to produce seed can result in population extinction (Cohen, 1966).

The dry weight allocation to "seeds" shown by these two species is within the boundaries for their respective reproductive strategies proposed by Ogden (1968) (Figure 14.1). The comparative dry weight allocations to sexual reproduction also show correlations with the r-K theory (see section 1.3), with the short, annual life history associated with high sexual reproductive allocation and the longer, perennial life history associated with low allocation to sexual reproduction.

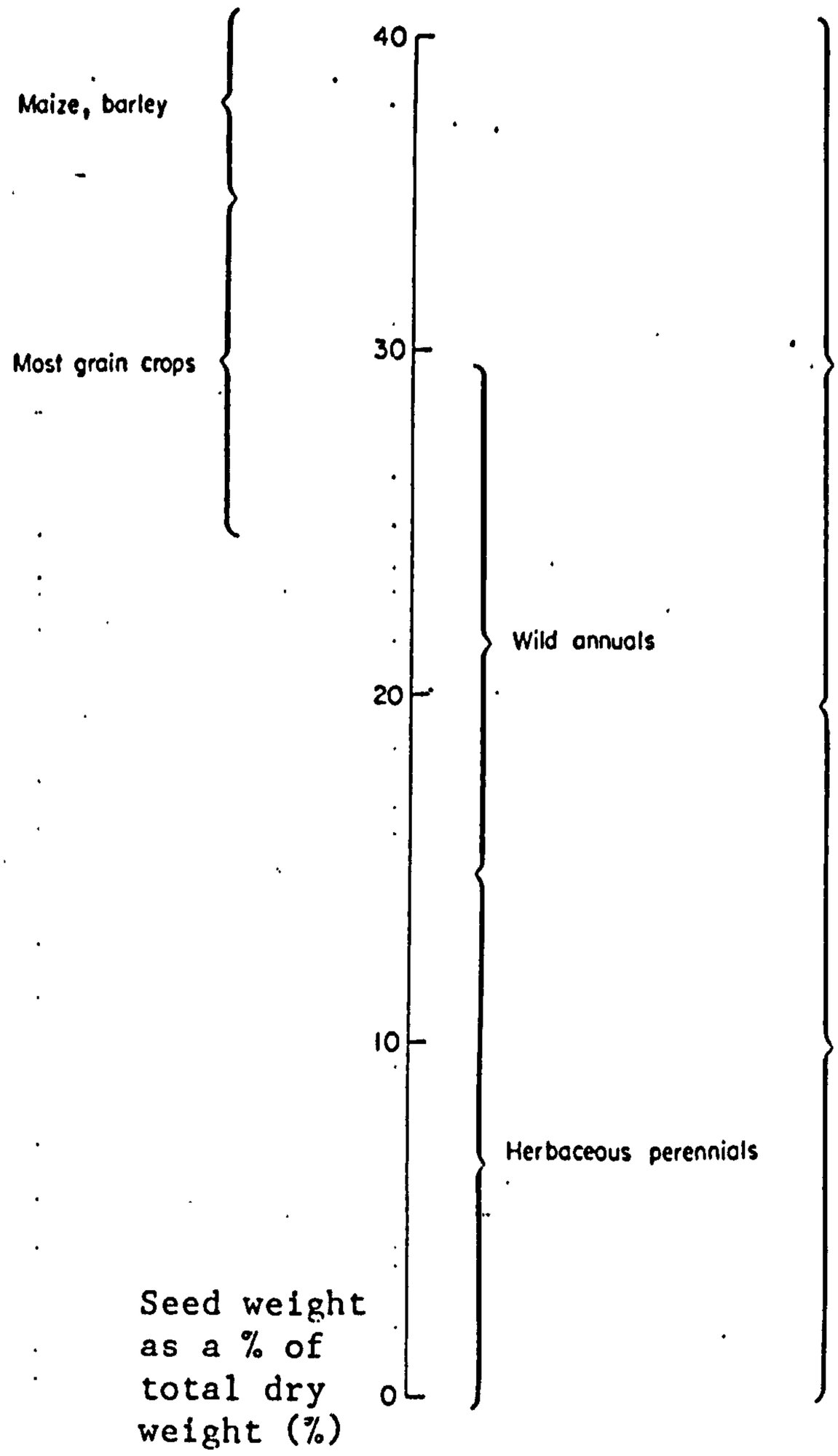


Figure 14.1

Dry weight of seeds as a percentage of total dry weight for various plant groupings (after Ogden, 1968).

The overall aim of this project was to study the ecology of *R. sceleratus* and *R. repens* in relation to seasonal submergence. This project has shown that submergence plays an important role in the ecology of both these species in habitats subjected to seasonal submergence.

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Appendix 1

Ranunculus repens Study Sites

"The communities in which R. repens plays an important part are .. disturbed soils .. grassland .. semi-aquatic communities .. and open patches .. in woodlands."

(Harper, 1957:316)

A1.1 Introduction

The three R. repens populations studied in Chapters 3 to 9 are from three different sites. Two of these sites are on Port Meadow, Oxford. The third is on the Open University campus at Milton Keynes. The following is a general description of the vegetation and environment at the three sites.

A1.2 Port Meadow Submerged Site

This site (Figure A1.1) is regularly submerged during winter and spring. This has taken place for many, probably hundreds of, years (Alison MacDonald, pers. comm; Baker, 1937; Harper, 1977). The vegetation is composed of a mixture of damp ground and semi-aquatic plants including: Agrostis stolonifera (d) (Cover of vegetation given on the DAFOR scale, i.e., d = dominant; a = abundant; f = frequent; o = occasional; r = rare; and l = locally), Ranunculus flammula (a), Apium nodiflorum (f),

River Thames

Roads

Railway

Port Meadow

Track running near the ditch

The ditch

Port Meadow R. repens study sites

Port Meadow ditch site for R. sceleratus study

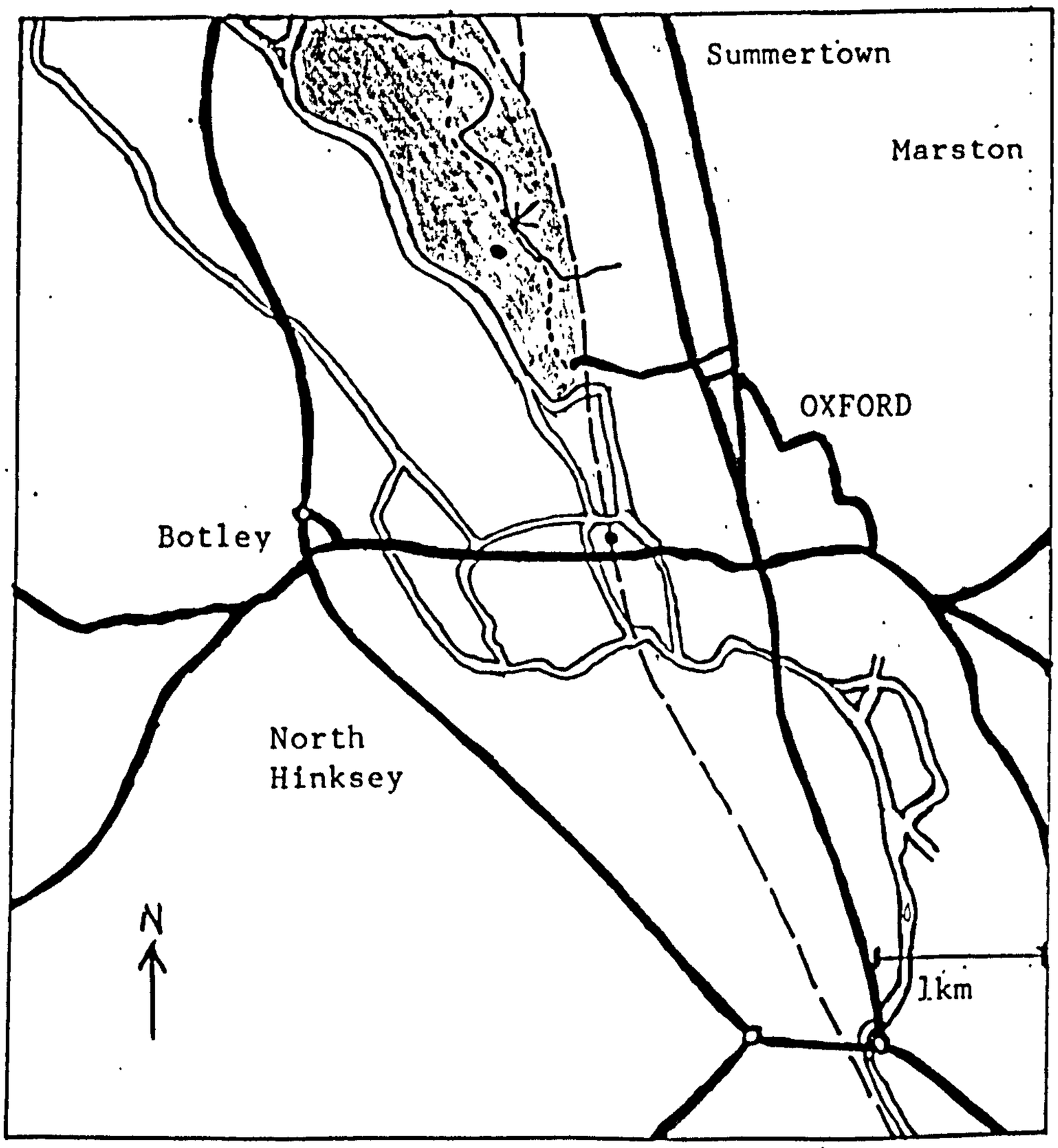

Figure A1.1

Plan of the Oxford area showing Port Meadow. The R. repens and R. sceleratus study sites are marked.

Trifolium fragiferum (la), Myosotis scorpioides (f), Rumex conglomeratus (la), Glyceria fluitans (f), Ranunculus repens (a), Mentha aquatica (a),

The site is grazed, and trampled, by cattle and horses when not submerged. Poaching by these animals can be quite severe, especially at the water's edge in late spring/early summer, as the water level falls. The plants at this site are rarely subjected to drought. In the long, hot summer of 1976 the vegetation was still green at this site (A. MacDonald, pers. comm.). Rainfall, and maximum and minimum temperatures for the Oxford area during 1982-1984, along with 30 year averages, are given in Appendix 2 (Figures A2.4 and A2.5). During 1983 this site was submerged from January to April.

A1.3 Port Meadow non-submerged site

This site (marked on Figure A1.1) is on a bank which rises from the Port Meadow submerged site. The earth which forms the bank was placed in its present position during the second world war, raising the level of the meadow in this area to prevent submergence (A. MacDonald, pers. comm.). The land was used for allotments during this war period.

The vegetation is that of a disturbed grassland; Lolium perenne (a), Cynosurus cristatus (a), Poa trivialis (a), Bellis perennis (a), Ranunculus repens (f), Ranunculus bulbosus (f), Ranunculus acris (r), Prunella vulgaris (o), Taraxacum officinale agg. (o), Cirsium arvense (o), Agrostis stolonifera (f), Trifolium repens (o), Urtica dioica (o), Trifolium repens (o), Plantago major (o), Poa annua (o).

The site is grazed, and trampled, by cattle and horses for much of the

year. Port Meadow (as a whole) is considered by many to be overgrazed (A. MacDonald, pers. comm.). The soil at this site appeared to be very dry from late June onwards in 1982 and 1983. In July 1983 the soil moisture level was 20-40% w/w compared to the submerged site (not submerged at the time) of 60-70% w/w. Rainfall, and maximum and minimum temperatures for the Oxford area during 1982-1984, along with 30-year averages, are given in Appendix 2.

A1.4 Open University site

This site is on the Open University campus in Milton Keynes, some 40 miles from Port Meadow (see Figure A1.2). The vegetation is typical of a disturbed grassland; Lolium perenne (a), Poa annua (a), Ranunculus bulbosus (o), Ranunculus repens (f), Plantago major (o), Plantago lanceolata (o), Bellis perennis (o), Holcus lanatus (f), Agrostis stolonifera (o), Festuca rubra (o).

The site has been subjected to considerable disturbance during the last ten years due to nearby construction work. The site is regularly mown (roughly 2 and 4 week intervals during the growing season) and never grazed. The site is often waterlogged in winter and dry in mid-summer. Rainfall, maximum and minimum temperatures recorded by the Meteorological station at Lathbury, about five miles north of the Open University site, for 1983 are given in Figures A1.3 and A1.4 along with 30-year averages.

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—.—. Railway
═══ Road
● R. repens study site

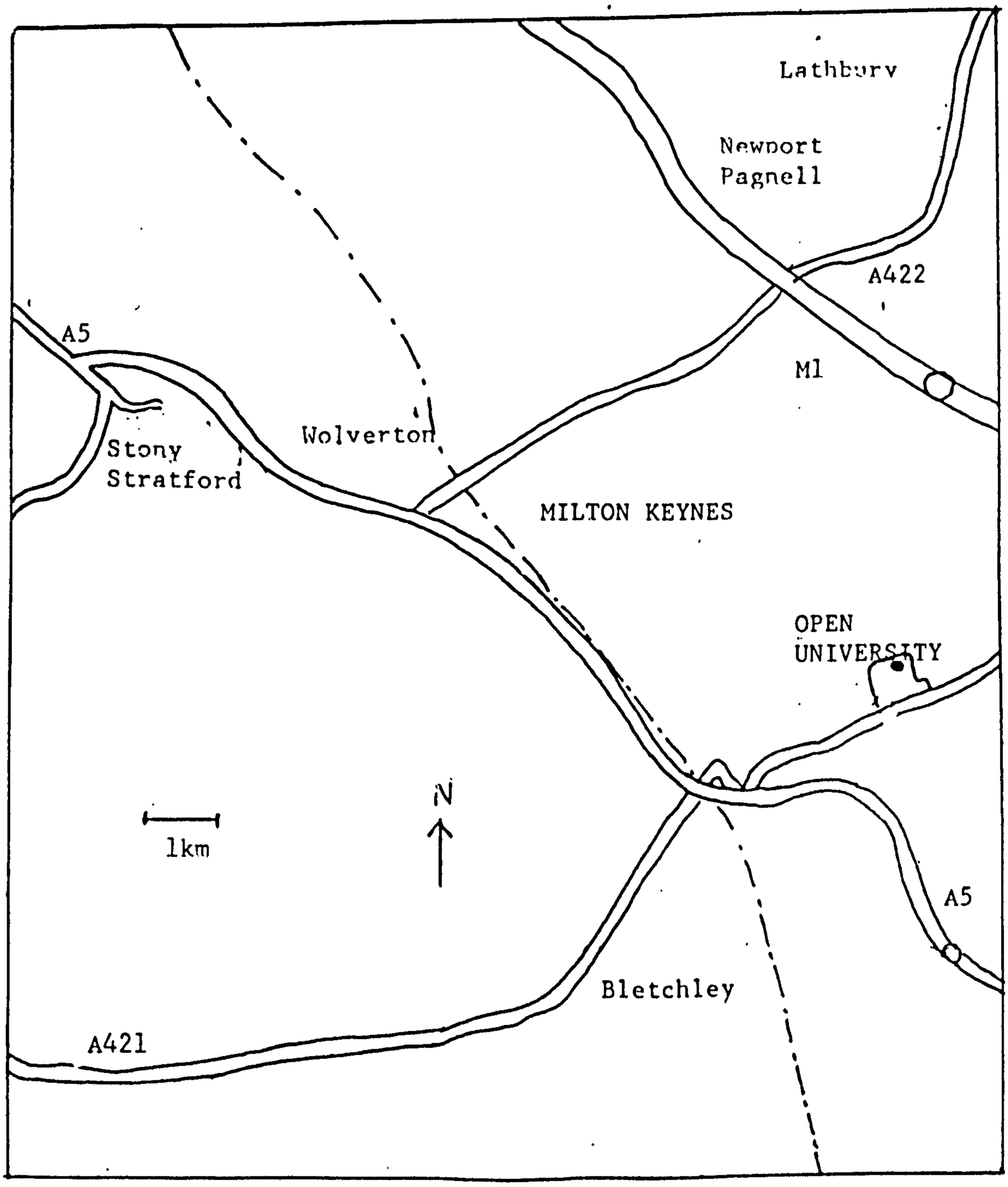

Figure A1.2

Plan of the Milton Keynes area showing the Open University campus at Walton Hall. The position of the R. repens study site is marked.

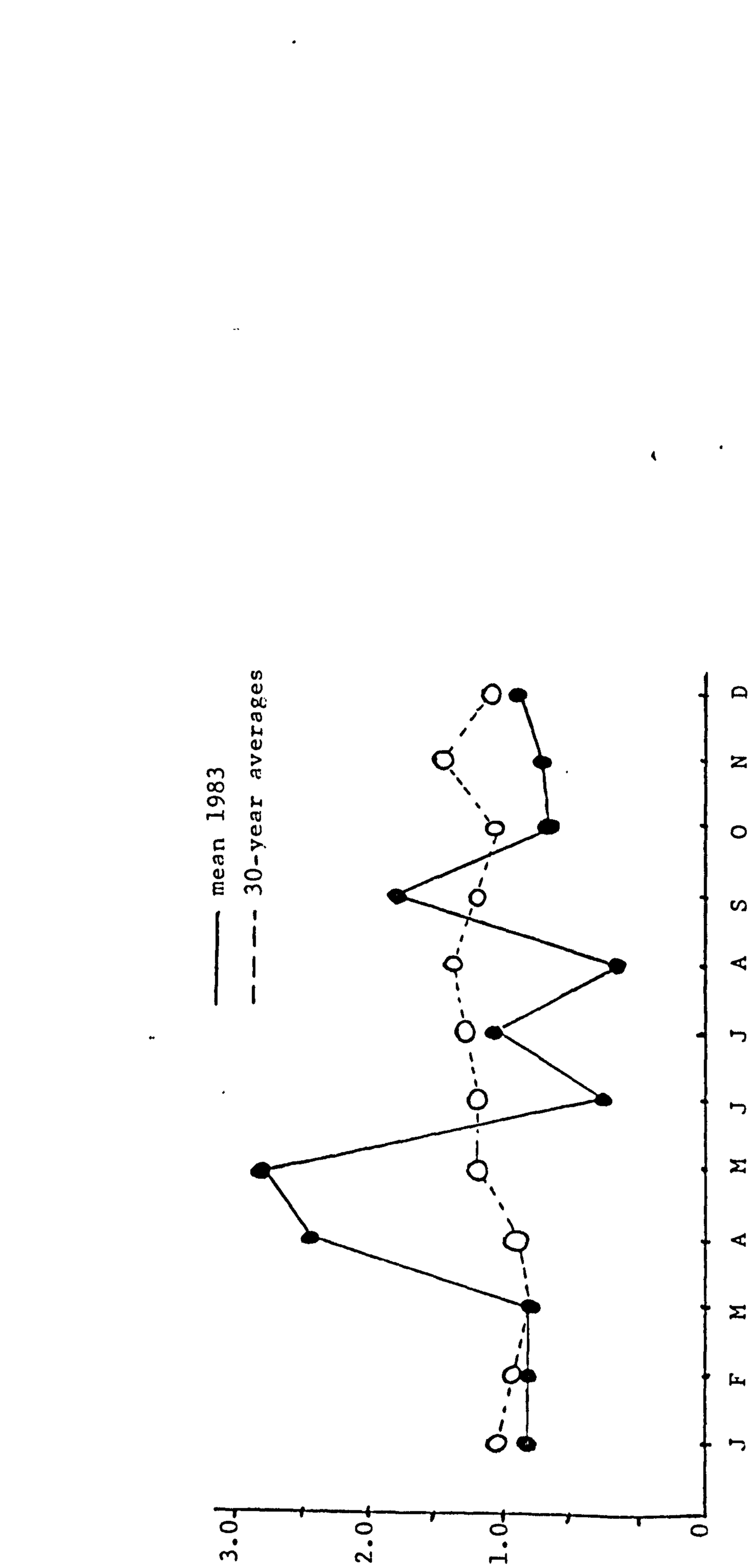

Figure A1.3

Daily rainfall on a monthly basis for 1983 and 30-year averages (1941-70) for the Milton Keynes area.

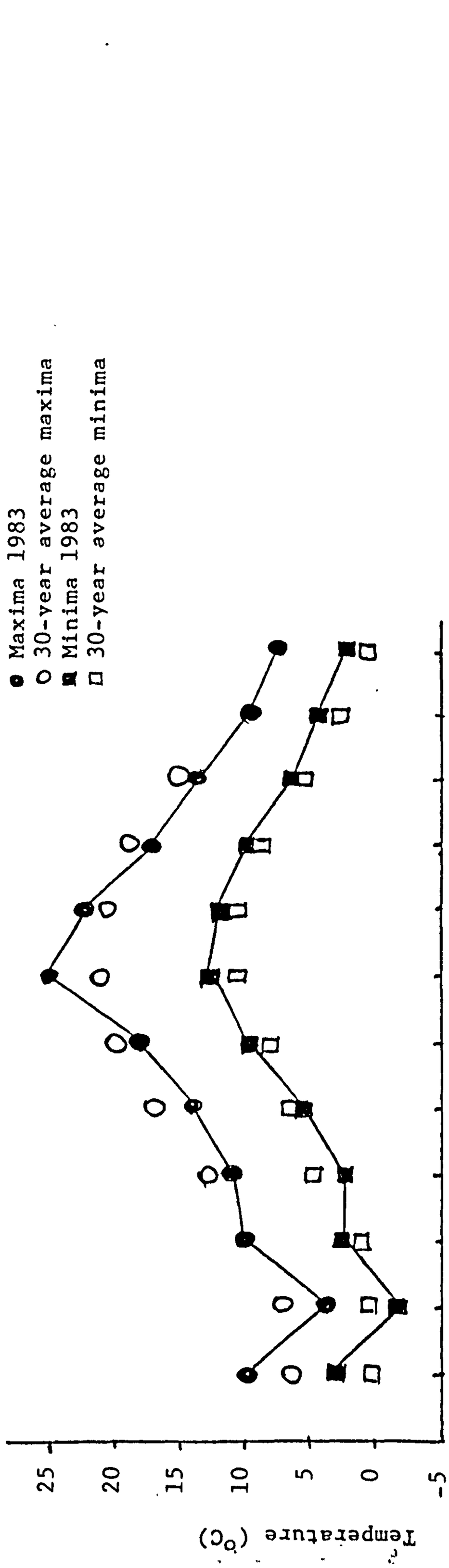

Figure A1.4

Maximum and minimum temperatures for 1983 and 30-year averages (1951-80) for the Milton Keynes area.

Appendix 2

Ranunculus sceleratus Demographic Study Site

"..Port Meadow .. has been grazed by cattle, horses and geese (no sheep) for nearly 900 years.."

(Harper, 1977:437)

A2.1 Description of Site

The demographic study of Ranunculus sceleratus was carried out in a drainage ditch on the eastern edge of Port Meadow, Oxford. The ditch is marked on the map shown in Figure A1.1, with the research site marked with an arrow. A cross-section of the ditch at this point is shown in Figure A2.1. Along the top of the ditch bank runs a track, this track being about 6m from the water's edge.

The track, apart from wheel ruts, consists of almost continuous vegetation. The dominant species are Festuca rubra, Lolium perenne, Poa annua, Poa pratensis, Ranunculus acris, Trifolium repens, and Trifolium pratense. The upper part of the bank, below the track, consists of similar nearly closed vegetation. At about 3m down the bank from the track the vegetation begins to open and other species are found. These are Rumex crispus, Rumex obtusifolia, Agrostis stolonifera, Ranunculus repens, Bellis perennis and Cirsium arvense.

Further down the bank the vegetation opens further until the upper vegetation disappears completely leaving a very open community of

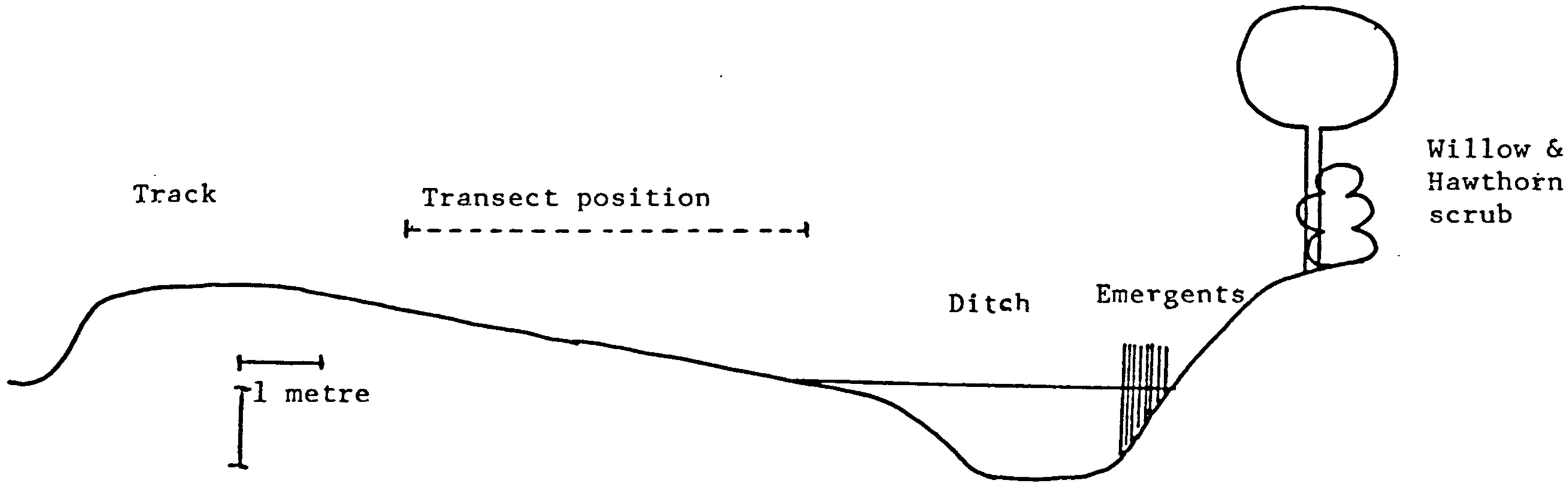

Figure A2.1

Diagra matic cross-section of the Port Meadow ditch site used for the demographic study of R. sceleratus.

Ranunculus sceleratus, Ranunculus repens, Agrostis stolonifera, Cardamine flexuosa, Veronica catenata, Apium nodiflorum, Scrophularia aquatica, Chenopodium rubrum and Mentha aquatica. Below the usual water level, about 6m from the track is a mixture of Glyceria declinata, Nasturtium officinale, Apium nodiflorum, Callitriche spp. and Lemna minor.

On the far bank, which is steeply sloping, is a line of Salix fragilis and Crataegus monogyna. Below this on the water's edge is a thin belt of emergents consisting of Typha latifolia and Carex riparia. The bank is covered with abundant Solanum dulcamara. The water level in the ditch changed with the seasons, the upper part of the bank being only rarely submerged and the bank below the normal water level rarely exposed to the air.

A2.2 Site Survey

The site was surveyed during Spring 1983 using two ranging poles, string and a line-level. This was achieved by tying the string at equal heights on the two poles and in situ re-levelling using a line level. The distance between the previous level position and the new level position on the ranging pole was equivalent to the change in height of the land between the two ranging poles. The levelling was carried out at 0.5m intervals down the three transects.

The results of the survey are shown in Figure A2.2 and show little difference between the three transects until quadrat 10 where transect A is lower than B which in turn is lower than C.

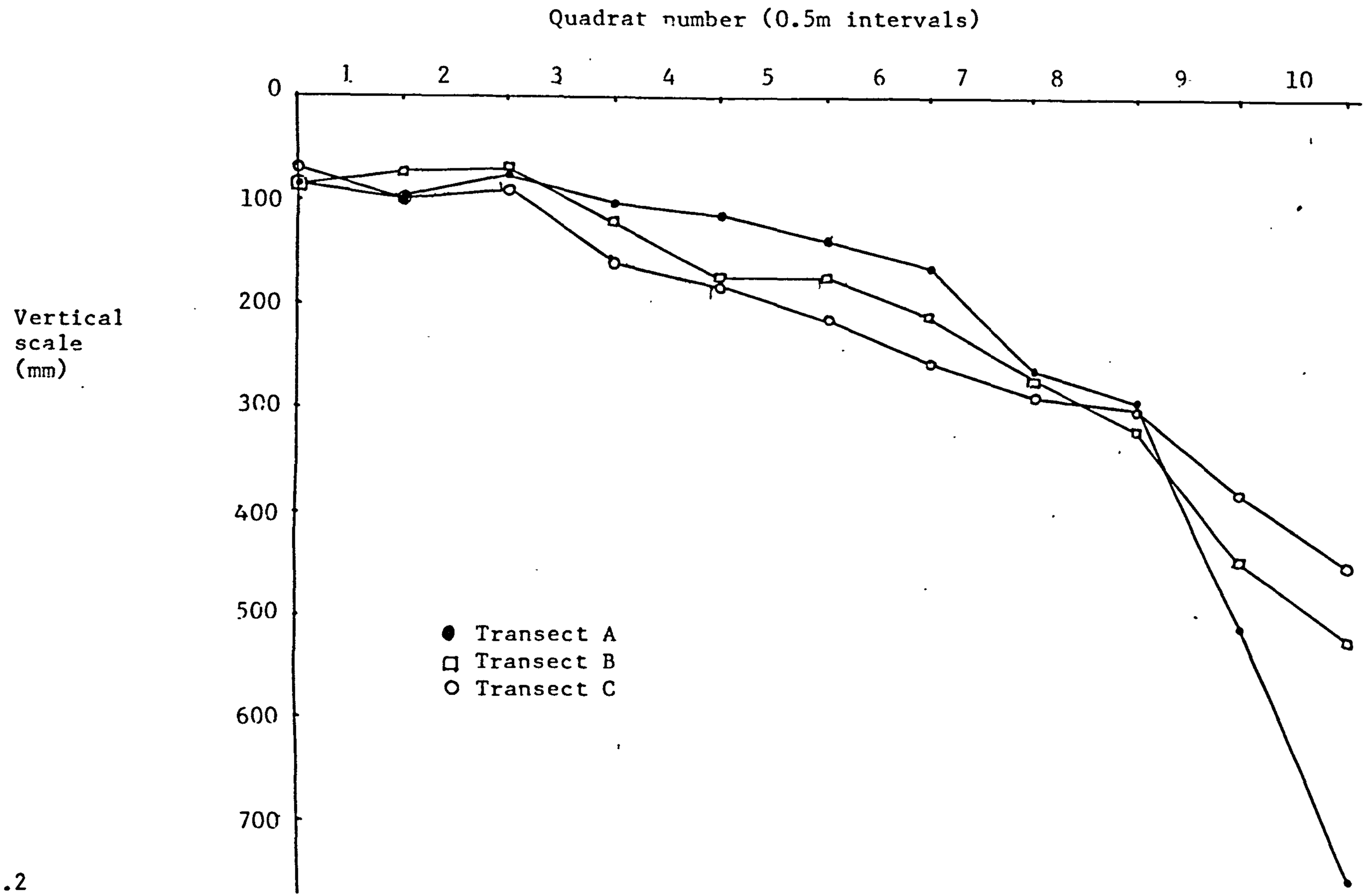

Figure A2.2

Height survey of the three Port Meadow ditch site transects used in the demographic study of R. sceleratus.

A2.3 Water levels

The water level data shown in Figure A2.3 are based on the position of the water's edge with respect to quadrats and not depth, although this data can be converted into depths using the survey data. Figure A2.3 can be used to see instantly how often a quadrat was submerged and for what period. It can be seen that the top of quadrat 10 (bottom of 9) can be considered as the usual water level, i.e. the ditch water level when there is neither drought nor flood.

One of the most striking features of Figure A2.3 is the unpredictability of both submergence and drought periods, both in terms of timing and length. This can clearly be seen by the fact that in May 1983 the study area was submerged, whereas in May 1984 it was droughted.

Overall it can be seen that the upper bank (quadrats 1-2) was submerged very little, the middle bank (quadrats 3-6) was submerged slightly more, whereas the lower bank (quadrats 7-9) was submerged for much longer. The quadrat 10s are below the 'usual' water level and were submerged for most of the study. Some idea of the amount of submergence experienced by each quadrat group can be gained from Table A2.1, which is based on Figure A2.3, and shows the percentage of time that each quadrat group was submerged during the whole study period.

A2.4 Temperature and rainfall data

Maximum and minimum temperatures (Figure A2.4), and rainfall measurements (Figure A2.5) for the area for the period of the study and the 30-year averages were obtained from the Meteorological station at Oxford, which is about one mile from Port Meadow.

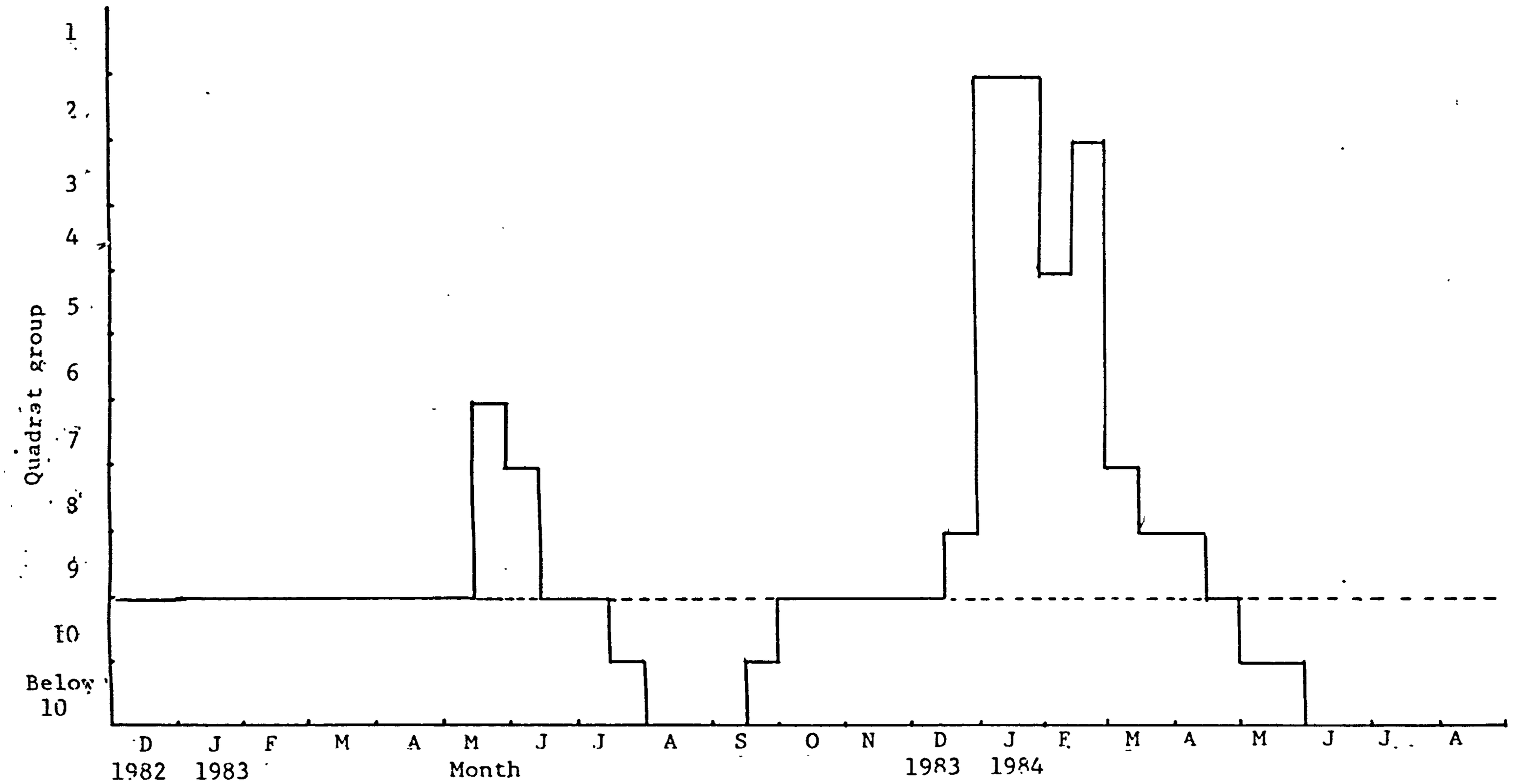

Figure A2.3

Water levels at the Port Meadow ditch site during the study period in terms of submergence of quadrat groups.

Table A2.1

The percentage of the study period (12/82 to 8/84) that each quadrat level at the Port Meadow ditch site was underwater.

Quadrat zone	% study period underwater
1	0
2	3
3	5
4	5
5	7
6	7
7	10
8	15
9	23
10	62

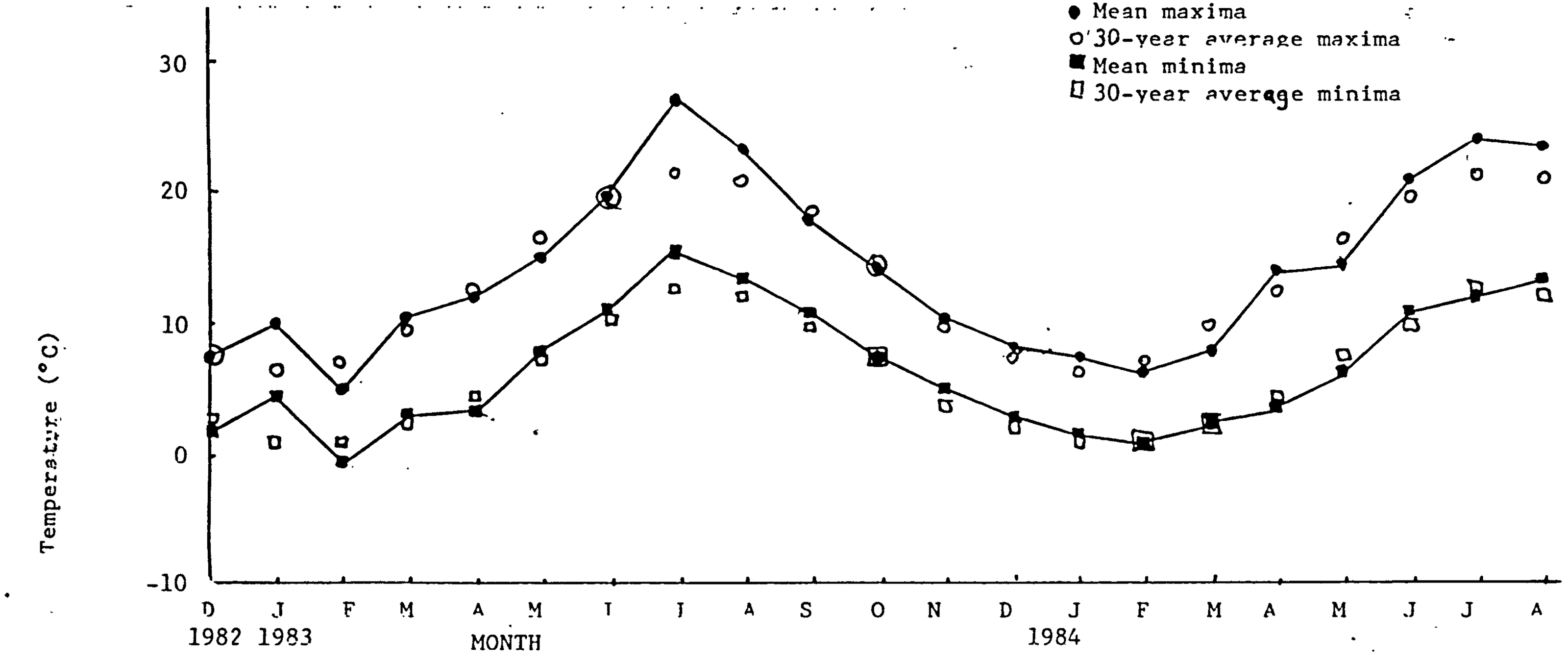

Figure A2.4

Maximum and Minimum temperatures for the Oxford Met. station (see text) during the study period and 30-year averages (1951-80).

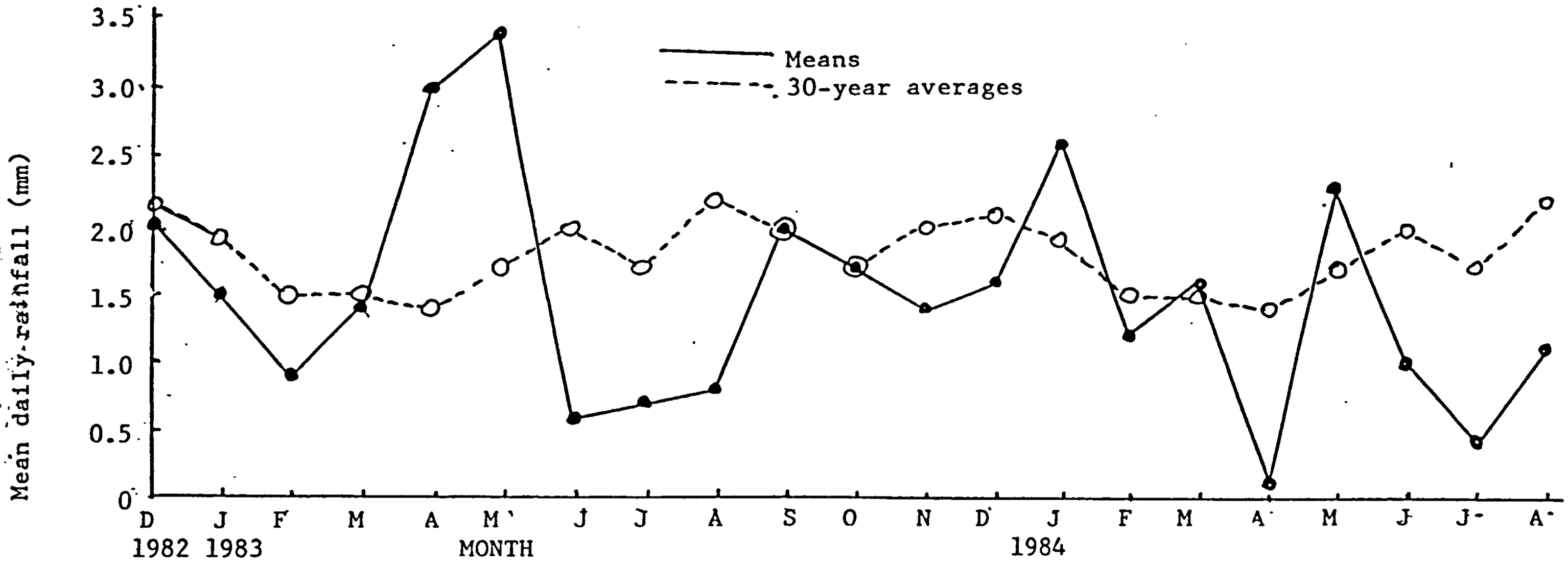

Figure A2.5

Average daily rainfall on a monthly basis for the Oxford Met. station during the study period and 30-year averages (1951-80).